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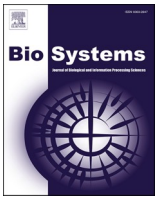

Full Length Article

The behavioural and socio-cognitive implications of the evolution of the primate predatory pattern: An embodied and integrative theory of human carnivory

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ABSTRACT

The article aims to unravel the elementary structures of hominin carnivory by drawing upon paleoanthropological, archaeological, primatological, and ethnographic investigations to underscore the primary differences and similarities in meat-eating patterns within the Primate order. Theoretically, it proposes a potential evolutionary scenario for a wide variety of carcass acquisition strategies—including highly embodied forms of associations with organismic kingdoms and inorganic matter—developed in our hominin lineage by comparing the behavioural and cognitive complex (i.e., tool use, cooperative hunting, meat sharing, and scavenging behaviour) exhibited by our primate relatives. This, at a more granular level, may shed light on the most basic forms of cognition, sociality, technical skills, and interspecies intimacy and relationalities that characterise the primate predatory pattern, which has further evolved into complex forms of animal-hominin entanglements deeply embedded in a niche filled with heightened levels of bodily interaction, sensory engagement, and perceptual experiences. From the analysis of these modes of embodiment in the animal-hominin interface, the theoretical model thus unveils the complex interplay between lower- and higher-order relational processes involved in patterns of meat consumption—from interspecies associations, bodily intimacy and compenetration of matter and intentionalities to forms of ritual, mytho-cosmological, and ontogical associations between humans, animals and and other agents from the physical and immaterial realms—which is manifest throughout the course of hominin evolution, thereby providing potential evolutionary templates to better understand human carnivory and its highly relational and embodied nature.

1. Unravelling the underlying evolutionary mechanisms of hominin meat-eating behaviour

The evolution of meat procurement strategies in the hominoid lineage is both a riddle and a fascinating matter. A diet based on vertebrate tissues has triggered in the genus *Homo* substantial morphological, physiological, metabolic, behavioural, and cognitive changes (Aiello and Wheeler, 1995; Milton, 1999; Stanford and Bunn, 2001; Mann, 2007; Antón et al., 2014; Pobiner, 2016; Leroy et al., 2023; Zhang et al., 2025) that permeate our evolutionary history. From the adaptation of Early Miocene apes (e.g., *Morotopithecus*) to feeding on leaves in Eastern Africa seasonal wooded grasslands (MacLatchy et al., 2023) to the Plio-Pleistocene emergence of stone toolmaking and carnivory (Domínguez-Rodrigo et al., 2005, 2021; Sahnouni et al., 2018; Cobo-Sánchez et al., 2022; Plummer et al., 2023), all these adaptive shifts likely point to ecological and nutritional factors as significant drivers of the evolution of our trophic and socio-cognitive niche.

Throughout the Plio-Pleistocene (~3 Mya), environmental and climatic variability and faunal turnovers may have caused strong selection pressures in our forebears, prompting the spread of Oldowan behaviour and thus facilitating the procurement of animal tissues (Plummer, 2004; Potts, 2012). This shift towards a diet rich in protein and fat likely caused a radical intellectual change in our genus since the brain increased in size (Aiello and Wheeler, 1995; Milton, 1999; but see Barr et al., 2022). Specifically, the emergence of *H. erectus* at ~1.8 Mya saw the evolution of morphological and cognitive traits leading to adaptive shifts in foraging and subsistence patterns (Leonard et al., 2007). Such biological changes (i.e., increase in body and brain size) in early *Homo* relative to *Australopithecus* signal the connection between its behavioural repertoire (i.e., tool use and social cooperation) and the procurement of high-quality nutrients (Antón et al., 2014). If, throughout hominin evolution, the reduction of the gut correlates with

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encephalisation, it became clear that in order to maintain an energetically expensive neural tissue, the assimilation of animal matter is critical (Aiello and Wheeler, 1995; Leonard et al., 2007). What, then, are the evolutionary, ecological, and socio-cognitive implications of this behaviour?

Whether the meat-eating strategies of ancient hominins reveal hunting or scavenging patterns is a matter of debate (Shipman, 1986; Pickering and Dominguez-Rodrigo, 2010; Dominguez-Rodrigo and Pickering, 2017; Thompson et al., 2019; Parkinson et al., 2022; Mateos et al., 2025); however, there are significant ecological consequences emanating from the extension of the trophic niche and the further incorporation of animal products into our ancestors' diet. For example, evidence suggests that Plio-Pleistocene carnivore extinctions in East Africa correlate with hominin exploitation of herbivores ranging from scavenging/kleptoparasitism to active hunting due to encephalisation and enhanced cognitive skills (Faurby et al., 2020). Also, the consumption of vertebrate tissues (mainly from mammals) by hominins and their close association with the carnivore guild may have triggered the incorporation of parasites such as *Taenia* tapeworms in their gut ecology (Henneberg et al., 1998; Hoberg et al., 2001; Hoberg, 2006). These trophic associations thus indicate that the assimilation of animal matter in early hominins has played a critical role in modelling modes of relations (predator-prey/host-parasite) and coevolutionary dynamics between taxa. Carnivory, in short, opened the way for complex biosocial relations, leading to significant evolutionary changes in the genus *Homo* (Foley, 2001).

Dominguez-Rodrigo and Pickering (2017: 19) argue that "hunting and meat-eating were among the basal adaptive strategies of the very earliest human ancestors." The authors, in turn, suggest that this behavioural module shared by humans, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) represents a "synapomorphy, rather than a homoplasy, of these sister taxa" (Dominguez-Rodrigo and Pickering, 2017: 8). Take this phylogenetic continuity concerning the behavioural and cognitive traits within the hominoid lineage. Although there are considerable ecological and technological differences between modern hunter-gatherers' and archaic hominins' meat procurement strategies (Ben-Dor et al., 2021), one might point out that an underlying neurocognitive structure may nevertheless operate in the carnivorous behaviour of these taxa. In effect, if we take these rudimentary socio-cognitive mechanisms, a wide variety of meat-eating strategies (e.g., tool use, cooperative hunting, meat sharing, scavenging behaviour) exhibited by archaic hominins and extant foragers may correspond, at least partially, with the carnivorous behaviour of non-human primates, e.g., chimpanzees (*Pan troglodytes*; Pruetz and Bertolani, 2007; Pruetz et al., 2015; Samuni et al., 2018; Nakamura et al., 2019; Pika et al., 2019; Achorn et al., 2023; Baker et al., 2024), bonobos (*Pan paniscus*; Surbeck and Hohmann, 2008; Fruth and Hohmann, 2018; Samuni et al., 2020), baboons (*Papio* spp.; Strum, 1975; Goffe and Fischer, 2016; Sommer et al., 2016; Davis et al., 2024; O'Hearn et al., 2025), and capuchin monkeys (*Cebus* and *Sapajus* spp.; Perry and Rose, 1994; Rose, 1997; Filho et al., 2021; Falótico, 2023; Bender and Aguiar, 2025).

While all these behavioural patterns point to several similarities in humans and non-human primates, there are considerable differences underlying the predatory behaviour of these taxa (Butynski, 1982b). A compelling explanation for this gap is that a new socio-cognitive niche, which evolved from the ancestral primate-like behavioural patterns, enabled humans to take a carnivorous position and deploy marked behavioural innovations (i.e., cooperation, egalitarianism, theory of mind, language, and culture) (Whiten and Erdal, 2012). It seems likely that both social and ecological factors might have played a pivotal role in the evolution of these cognitive faculties. For example, the social-brain hypothesis suggests a correlation between relative brain size and primates' different degrees of social complexity (Dunbar, 1998). It is this complex level of sociality (e.g., demographic increase), coupled with brain expansion, that probably has enabled Acheulean hominins (~1.5 Mya) to occupy a high trophic level as big game hunters (Dominguez-Rodrigo and Pickering, 2017). Ecologically speaking, incorporating animal matter was likely a direct response to Pleistocene environmental fluctuations as hominins began deploying innovative cognitive solutions and foraging behaviours to explore new dietary niches (Kaplan et al., 2000).

It might be said that, among extant primates, only humans and panins share a common behavioural adaptation (viz., a synapomorphic trait) to a carnivorous diet (Dominguez-Rodrigo and Pickering, 2017) and show complex social systems. Their behavioural and cognitive qualities might thus differ in degree but not in kind, and hence, social and ecological selection pressures may have played a vital role in their evolution. In order to tackle the basic tenets of hominin carnivory, one should thus first elucidate its evolutionary pathways and the behavioural, ecological and socio-cognitive implications associated with different levels of relations with animal taxa exhibited by the primate order.

This paper then attempts to delineate the elementary structures of human carnivory, drawing upon paleoanthropological, archaeological, primatological, and ethnographic investigations to highlight the main differences and commonalities in meat acquisition patterns within the primate order. It also suggests a possible evolutionary scenario for the different modalities in meat-eating behaviour developed throughout hominin evolution, thus bridging the gap between primary forms of carnivory exhibited by extant primates (Watts, 2020) and evolved forms of animal-human associations (Shipman, 2010). This is based on the following theoretical assumptions. First, a comparison of the behavioural and cognitive complex (i.e., tool use, cooperative hunting, meat sharing, and scavenging behaviour) within and between primate species may shed light on the most basic cognitive, social, and technical skills for meat acquisition. Within this comparative framework, therefore, specific forms of primate-prey interactions may reveal varying degrees of interspecific bodily contact, socialisation and sensory and cognitive engagement; different levels of relationships with animal matter—from elements of tool-assisted predation to prosocial forms of meat acquisition strategies—may be framed as potential precursors of a complex constellation of behaviours and cognitive abilities that developed patchily and gradually among our hominin ancestors.

Second, based on the varying degrees of meat-eating behaviour and contact intensity (bodily interactions and sensory-cognitive engagement) with animal tissues shown by primates, I hypothesised that, as far as predatory carnivory has been internalised gradually in the *Homo* lineage, relations with prey taxa necessitated higher-order categories of representation as meat-eating strategies became more cognitively demanding and sophisticated. As such, the immersion into the predator guild (and hence the acquisition of large animals) not only provided early *Homo* with high-value protein, fat, and micronutrients but also served as material affordances for the emergence of elevated forms of multispecies intimacy, techno-behaviour, socialisation and sense-making processes. This, as it turns out, unfolds the enhancement, amplification, and complexification of the predatory pattern of non-human primates.

Third, as a corollary, I postulated that forms of ritual behaviour—particularly those associated with Palaeolithic hominins and large mammalian species (i.e., rock art, special treatment of animal skeletal remains and body parts)—were likely infused with mytho-cosmological and ontological dimensions. These behavioural patterns and emergent conceptual schemas may have operated as superstructural mechanisms aimed at the accentuation of animals' agentic and metaphysical properties, which likely modulated specific interlinkages and negotiations with prey and other entities—from food taboos to shamanic and spiritual mediations acting as regulatory devices for the respect and preservation of prey—that further achieved their maximum manifestation among modern foraging societies. This complex behavioural and cognitive repertoire that emerged among Palaeolithic hominins and subsequently became firmly established in contemporary hunter-gatherers not only uncovers particular patterns of associations with

animals (as in the case of those with extinct and extant megafauna) but also propels the rethinking of the evolution of carcass acquisition strategies as inextricably intertwined with heightened forms of interspecies intimacy, bodily interactions, sensory engagement, social and emotional bonding—a wide variety of phenomenal experiences and subjective qualities may have been triggered by these relational processes. Thus, modes of theorising on animals—namely, conceiving animal matter beyond its nutritional and utilitarian significance—I suggest, were likely heavily dependent on these aspects.

Lastly, and in light of the above-mentioned premises, my ultimate aim is to provide an analytical and comparative framework concerning the elementary structures of primate carnivorous behaviour. The examination of these varying patterns of predation may help reconstruct prehistoric forms of association with animals, thereby providing potential evolutionary templates and valuable insights into the evolution of human carnivory, whose highly relational and embodied dimensions have further incorporated abstract forms of thinking and higher-order modes of relation.

2. Embodiment and cognition in primate and hominid carnivory

Before examining patterns of meat acquisition in non-human primates, a brief overview of the evolutionary pathways of hominin carnivory is needed to better situate our analytical framework. This, in fact, would serve as an analytical tool to outline relational and embodied forms of carcass acquisition strategies that (*i*) have gradually evolved in the primate lineage, displaying discernible patterns of predatory-prey interactions, distinct levels of interspecies intimacy and sociality; and (*ii*) have ultimately revealed the emergence of a foraging niche deeply embedded in multi-layered relational processes and centripetal forces involving complex trophic and social interactions and revolving around the modification, assimilation, and compenatration of matter.

2.1. A brief overview of patterns of predation

A growing body of evidence from primatology has unveiled a wide variety of meat consumption patterns in non-human primates (Watts, 2020); however, chimpanzees and bonobos, our closest biological relatives, stand out among extant non-human primates as the most carnivorous species (Dominguez-Rodrigo and Pickering, 2017). Building upon these behavioural data, a series of inferential arguments has developed to reconstruct the predatory behaviour and forms of carcass acquisition strategies likely exhibited by hominoids of the deep past. For example, it is assumed that the last common ancestor of *Pan* and *Homo* probably engaged in hunting and meat-eating activities (Dominguez-Rodrigo and Pickering, 2017; Wood and Gilby, 2017). Archaic hominids like *Ardipithecus ramidus* may have captured prey through somatic means (viz., by hand, either on the ground or in trees), a pattern similar to chimpanzees (Stanford, 2012: 145). Likewise, taking chimpanzees as referential models, Pickering and Dominguez-Rodrigo (2010: 110) argue that "pre-lithic hominids likely hunted small animals, which did not require extrasomatic processing to consume." Contrary to the small-animal hunting patterns exhibited by chimpanzees and possibly pre-lithic hominids, it is believed that scavenging on large-animal carcasses was the newly introduced prey-acquisition strategy employed by hominins aimed primarily at the exploitation of marrow (fat) rather than flesh (protein) (Blumenschine, 1991). In the Pliocene, with basic percussive technology, this foraging behaviour may have indeed provided hominins access to within-bone nutrients rich in fat from these large-animal resources (Thompson et al., 2019). This emergent techno-behavioural pattern therefore clearly departs from the proto-percussive technology documented among chimpanzees to exploit the inside-bone nutrients of small-animal carcasses (e.g., Boesch and Boesch, 1989; Pika et al., 2019). In light of the aforementioned considerations, it is not surprising that the assimilation of animal matter and its rich packages of macronutrients and micronutrients (e.g., protein, fat, iron, zinc, vitamin A, vitamin B-12) (Murphy and Allen, 2003; Ben-Dor et al., 2021) was likely the driving force behind both scavenging and hunting patterns among early hominins.

While incorporating high-quality animal products may have been the primary biological determinant for our ancestors' adaptive shift in dietary patterns, little is known about the relational processes—bodily and cognitive engagement between agents—involved in those trophic associations. Speculatively, hominin carnivory may likely have emerged as a highly relational embodied activity (be it hunting or scavenging) of meat acquisition in which the processes of tracking, chasing, stalking, touching, killing, butchering (cut and percussion), and chewing of animal bodies triggered a myriad of sensible qualities exemplified in the modification and assimilation of matter (i.e., bones, flesh, marrow, blood, and other body fluids). This ancient behaviour thus indicates complex patterns of adaptation and cognitive engagement with physicalities that provided the means for dietary expansion (Plummer et al., 2023), introducing significant quantitative and qualitative changes throughout hominin evolution (Isaac, 1978; Aiello and Wheeler, 1995; Stanford, 1999; Navarrete et al., 2011).

Archaeological evidence from Nyayanga, Kenya, suggests that nearly 3 Mya *Paranthropus* sp. could have made stone tools and butchered animal carcasses—including megafauna like hippopotamid taxa (Plummer et al., 2023). Hence, this archaic hominin would have modified abiotic and biotic components (making stone tools and processing large-animal carcasses) and assimilated significant biological properties epitomised in high-quality animal products. It is thus highly likely that *Paranthropus* was dynamically engaging in a higher trophic level (although sporadically), exploiting the benefits of nutritional elements derived from consuming meat and marrow. Even if environmental fluctuations were strong selection pressures for a dietary shift in ancient hominins, the socio-ecological implications for even the lowest degree of carnivory might have been substantial. As such, within specific environmental constraints, the emergence of hominin carnivory could have opened the way for new ecological relationships where varying agentive forces modified and assimilated each other. Carnivory, conceived here as the highest degree of bodily exposure (interspecific physical contact and co-contamination of bacterial and parasitic agents), likely exerted a significant cognitive load in early *Homo,* causing the selection for novel cognitive skills as the brain increased in size (Kaplan et al., 2000). The evolution of human cognition would therefore likely have relied substantially on centripetal relational processes that stemmed from the most basic exchanges of entities' bodily compounds.

2.2. On animal-hominin relationalities

Let's elaborate on the relational processes involved in the carnivorous dietary niche of ancient hominins. Imagine a group of Pliocene ancestors scavenging on a large animal carcass left by sabretooth felids. There, they were pounding the bones with stones and tree boles to obtain marrow. While relishing the package of inside-bone nutrients (Thompson et al., 2019), they confronted other agentive forces immersed in the same spatio-temporal dimension of trophic interactions. From pathogenic bacteria and parasites circulating in animal matter to maggots feeding on the putrefying corpse to other carnivores and scavenger animals, this wide array of taxa was most likely in close contact with our archaic relatives. Take, for example, another Pliocene scenario in which *Australopithecus afarensis* (~3.39 Mya) was both cutting and pounding with stone tools the bones of a large ungulate to obtain flesh and marrow (McPherron et al., 2010). Under these potential circumstances, a similar pattern of multispecies encounters—from microorganisms to apex predators—may have arisen from even the most basic form of subsistence strategies. Alternatively, even in the case of pre-lithic hominins (e.g., *Ardipithecus ramidus*) who, as putative hunters like chimpanzees, may have preyed upon small animals (Pickering and Dominguez-Rodrigo, 2010; Stanford, 2012), the relational pattern of interspecific interactions (albeit probably to a lesser degree) would

likely have caused in the former a considerable intensification of relational and cognitive processes.

Two hypothetical consequences might have emerged from the highly embodied and relational activity of meat acquisition among early hominins. Firstly, there was likely a simultaneous intensification of both the assimilation of high nutritional values and the degree of cognitive abilities employed in procuring animal matter. Indeed, hominin carnivory and its high degree of bodily immersion in specific socio-ecological interactions (from the tracking to the consumption of prey taxa) may have involved complex relational processes between organic and inorganic matter (e.g., Finkel and Barkai, 2024b). Different agents (from parasites and bacteria to predators and scavengers to plants and stone tools) may thus have been engaged in the processing and consumption of animal carcasses. This, coupled with hominins' highly multisensory engagement with animal tissues and fluids and the incorporation of high-quality nutrients, would likely have selected for increased cognitive capacities.

Secondly, a complexification of socio-structural patterns likely occurred through the process of meat acquisition from large animals. According to Ben-Dor and Barkai (2020), unlike small and medium-sized animals, large animals would have yielded high-fat content and high energetic return, requiring only rudimentary technology to obtain their nutritional properties. Percussion scavenging among Pliocene hominins is just a clear picture of how elementary forms of large-animal exploitation might have triggered complex social relations, such as intergenerational and cross-gender cooperation between group members in butchering activities (Thompson et al., 2019: 9). While preying upon small animals could have exerted significant selection pressures in the socio-cognitive niche of the earliest hominins, the implications for the evolution of higher levels of sociality must have been constrained by the small amount of animal matter available to consume and socialise (Pickering and Dominguez-Rodrigo, 2010; Stanford, 2012). On the other hand, the acquisition of megafauna taxa was likely a primary evolutionary driver of novel behavioural and cognitive capabilities as hominins began to immerse in highly embodied relational processes (via cooperative butchering, meat sharing, carcass patrolling, and perhaps some forms of reciprocal exchanges) that enabled both the incorporation of abundant nutritional components and the amplification of levels of sociality—primarily due to a large amount of available animal matter (Linares Matás and Yravedra, 2021; see also Dominguez-Rodrigo et al., 2026). The nucleation and socialisation patterns stemming from these archaic forms of animal-hominin associations (Linares Matás and Yravedra, 2021) would therefore likely have laid the groundwork for the further expansion of sophisticated social structures—typified by elevated meat sharing practices and other prosocial behaviours connected with the acquisition of animal-based resources that sculpt mating systems and intergroup bonding—, as those exhibited by modern hunter-gatherer and hunter-horticultural societies (Siskind, 1973; Wiessner, 2002; Gurven, 2004; Gurven and von Rueden, 2006; Koster, 2011; Wood and Marlowe, 2013; Dyble et al., 2016; Abad Espinoza, 2025; Abad Espinoza and Fleck, Forthcoming). Unarguably, these forms of meat procurement strategies and related behavioural and socialisation schemes far exceed those exhibited by non-human primates (Mitani and Watts, 2001; Gomes and Boesch, 2009; Fruth and Hohmann, 2018; Samuni et al., 2018; O'Hearn et al., 2025).

It has been suggested that the extinction of megafaunal taxa—bonanzas of meat, fat and other organic materials—during the Pleistocene may have been an ecological agent of selection for evolutionary changes (the transformation of a wide array of behavioural, technological, and cultural traits), driving humans to specialise in acquiring smaller prey (Ben-Dor and Barkai, 2021, 2023, 2024,2025b; see also Litov et al., 2026 for a compelling analysis of the Paleolithic Levant). Nevertheless, the specialisation in hunting skills and technological innovations for acquiring small taxa was likely contingent on ancient cognitive and behavioural patterns that stemmed from high levels of contact intensity with abundant animal matter. The importance of megafauna may therefore lie in the capacity for complex socialisation that hominins must have implemented for the modification (butchery and meat sharing) and subsequent assimilation (commensality) of large quantities of animal tissues. One might speculate that, unlike our primate relatives, which mainly acquire small prey relative to their body size, the human capacity to engage with big animals may have selected for the evolution of cognitive abilities ranging from sociality to abstract thinking. To further provide a thorough analysis of the evolutionary trajectories of human carnivory, we should primarily delve into the elementary behaviour patterns shared by the Primate order. As we shall see, by scrutinising primates' meat-eating strategies, we may perhaps reconstruct archaic cognitive faculties (those likely shared by our last common ancestor) that ultimately developed into the human predatory and socio-cognitive niche.

3. Primate cognition and the elementary structures of carnivory

What fundamental behaviour patterns are involved in meat-eating strategies among the primate species? To openly say that complex forms of cooperative hunting, meat sharing, and tool use set humans apart from the great apes is to provide evolutionary explanations without unravelling the most basic forms of primate behaviour and cognition. Phylogenetically speaking, the question of behavioural commonalities found in primates in general and hominins in particular likely indicates an underlying cognitive structure allocated in these species.

Against this background, and for the sake of clarification, the terms' elementary,' 'low-level,' and 'high-level' carnivory are used in this section as analytic heuristic devices to help outline the varying degrees and intensities of meat consumption exhibited by primates. Concerning the aforementioned levels of carnivory—as further shown below—for example, behavioural data suggest that instances of meat-eating behaviour among orangutans (*Pongo* spp.*:* Sugardjito and Nurhuda, 1981; Utami and van Hooff, 1997; Hardus et al., 2012; Buckley et al., 2015) are rare (low-level carnivory), while a more regular pattern of meat consumption is well-documented among chimpanzees (*Pan troglodytes:* Stanford, 1995; Pruetz and Bertolani, 2007; Fahy et al., 2013; Gilby and Wawrzyniak, 2018) in all their ecological habitats (high-level carnivory). Significant variations are also found between snub-nosed monkeys (*Rhinopithecus* spp.: Zhao et al., 2008; Ren et al., 2010) and capuchin monkeys (*Cebus*, *Sapajus:* Perry and Rose, 1994; Rose, 1997; Falótico et al., 2018; Filho et al., 2021), which show highly sporadic (low-level carnivory) and more frequent forms of carnivorous behaviour (high-level carnivory), respectively.

Unless future observations reveal new occurrences of meat-eating behaviour and, consequently, an increase in the level of intensity of carnivory among some primate species, the present conceptual framework may provide instructive cues about intra- and interspecific variations in meat consumption patterns. These low and high levels of carnivory are, however, likely founded upon elemental morphological traits, behavioural modalities, and cognitive qualities shared by the primate lineage. The elementary structures of carnivory (exemplified by emergent forms of predator-prey interactions, bodily contact, and sensory engagement with animal matter) are therefore the evolutionary roots of primate carnivorous behaviour, linking various configurations of meat acquisition strategies with their predatory prototype.

Interestingly, consistent with the behavioural prototype outlined above, a molecular phyloecological study shows that selective pressures for increased carnivory (i.e., insectivory) in the common ancestor of living primates were likely critical factors for adapting to ambush predation in arboreal environments (Wu et al., 2022). These, in turn, may have been the evolutionary determinants for the modern primates' bauplan since particular characteristics (i.e., convergent orbits, leaping, grasping hands and feet, and reduced claws) would have enabled the common ancestor of living primates to ambush its prey in trees. (Wu et al., 2022). Furthermore, a recent study about the evolution of

primate social organisation indicates that, unlike the long-held assumption that the ancestor of all primates was a solitary species, this may have exhibited flexible pair-living patterns (Olivier et al., 2024). This specific social organisation was likely an ancestral behavioural pattern from which more complex forms of primate sociality evolved (Olivier et al., 2024). Taken together, these lines of evidence stress the complexity of primate evolutionary history and its ecological and socio-cognitive implications for the evolution of different forms of meat procurement strategies and social behaviours exhibited by our fossil and living relatives. Insectivory, thought of as the likely earliest form of carnivory exhibited by the Order Primates (O'Malley and McGrew, 2014; Wu et al., 2022), is a very particular aspect of carnivorous behaviour that I will briefly explore to make sense of how a multiplicity of patterns of predation and modes of bodily interactions and cognitive engagement with animals may have emerged from this basic element of faunivory.

3.1. *Patterns of insectivory*

A wide variety of species of insects are routinely consumed by non-human primates and traditional societies around the world (McGrew, 2014; O'Malley and McGrew, 2014; Van Huis, 2017). Nutritionally, these organisms are significant sources of high-quality fat, protein, vitamins and minerals (O'Malley and Power, 2012; McGrew, 2014); it is therefore not surprising that living primates from baboons to orangutans and gorillas (*Gorilla*) to chimpanzees and human foragers feast on these nutrient-rich animal-based resources (Rhine et al., 1986; Fox et al., 2004; Deblauwe and Janssens, 2008; Bogart and Pruetz, 2011; O'Malley and Power, 2012; McGrew, 2014; Van Huis, 2017; Auger et al., 2023). Concerning the nutritional significance of insect-eating among non-human primates, Rhine et al. (1986) reported that grasshoppers (Orthoptera: Acridi) are the primary source of dietary protein for yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Likewise, among the orangutans at Suaq Balimbing, Sumatra, Indonesia (Fox et al., 2004), as among the Kasekela chimpanzees of Gombe National Park, Tanzania (O'Malley and Power, 2012), protein- and fat-rich insects (mainly those from the Orders Isoptera [termites] and Hymenoptera [ants, bees/honey]) are regularly ingested. It is from these eusocial insects that great apes obtain not negligible nutritional components comparable to those from vertebrate matter (O'Malley and Power, 2014); feeding on insects is not only a matter of macronutrient and micronutrient intake, however. Insectivory indeed entails high levels of sensorimotor intelligence and patterns of culturally transmitted behaviours and technical skills, as exemplified by forms of tool-aided extractive foraging exhibited by some primate taxa (e.g., *Pan troglodytes:* Bogart and Pruetz, 2011; O'Malley and Power, 2014; Pascual-Garrido et al., 2025; Sánchez-Megías, 2026; *Pongo pygmaeus:* Fox et al., 2004; *Sapajus libidinosus*: Mannu and Ottoni, 2009).

Before consumption (and hence the assimilation of insects' nutritional properties), lower-order relational processes are at stake within patterns of primate-insect associations. Forms of tool-assisted insectivory exhibited by the abovementioned primates thus underline complex multispecies entanglements and intimacies. The modification of a wide variety of plant taxa for the crafting of tools—and their subsequent utilisation in insect predation—not only points at high levels of behavioural flexibility, adaptation to ecological conditions, and transmission of cultural traditions (Mannu and Ottoni, 2009; Bogart and Pruetz, 2011; O'Malley and Power, 2014; Fox et al., 2004; Pascual-Garrido et al., 2025; Sánchez-Megías, 2026) but may also hint at a niche filled with elevated embodied engagement, multi-sensory experiences, and interspecies interactions. Similar centripetal forces and associated interspecies relationalities may also have been involved in the predatory niche of early hominins. The likely use of bone tools to prey on termites by *Paranthropus robustus* in South Africa (Backwell and d'Errico, 2001; 2008) is a prominent case of these embodied organismic interactions; as such, organic matter (bone, plants) likely played a foundational role in patterning insect-hominin associations, thus underlining the primacy of these elements as precursors of stone-tool technology (Pascual-Garrido et al., 2025).

The ingestion of energy-rich invertebrates (e.g., termites)—providers of critical nutritional components comparable to those from mammalian meat—may therefore have sparked substantial evolutionary changes (e.g., encephalisation) in the hominin lineage (Brömme et al., 2026). Also, Melin et al. (2014) postulated that the seasonal predation on insects—contingent on variable ecological and climatic conditions and periods of fruit scarcity—likely played a crucial role in the evolution of sensorimotor intelligence and associated traits (i.e., tool use, manual dexterity, and laterality) in primates in general and hominins in particular. Entomophagy, according to a recent research conducted by Piñero and Librado (2026), must have been a strong ecological pressure for enhanced chitin digestibility among Neanderthals, as well as among populations living in tropical regions characterised by insect abundance—a pattern in stark contrast with the low chitin digestibility of pre-agricultural and current European populations, lending further support to the religious cultural aversion towards insect consumption. The elevated nitrogen isotope ratios (δ15N) observed in Neanderthals, likely due to the regular consumption of putrefied animal matter infested with bonanzas of fly (Diptera) larvae (Beasley et al., 2025; see also Piñero and Librado, 2026), is an outstanding example of how fat-rich maggots may not only have played a key role in the trophic ecology of Neanderthals but also likely instantiated enmeshments of materialities and profound interspecific encounters.

Within this evolutionary framework, lower-order relational processes and associated multispecies relationships, as well as forms of embodied and sensory engagement, may have further shaped higher-order modes of relations with insects. Noteworthy in this regard is the role of termites in shaping the nutritional ecology and ritual and mythocosmological system of the San hunter-gatherers (Mguni, 2006). That is, aside from being considered a fat-rich food, termites and termite nests are the epitome of spiritual potency (equated with fat), transformative and generative powers and act as connectors of different ontological realms, as shown by San rock art and religious ideology (Mguni, 2006). So, if insectivory—as a basic element of carnivory and likely evolutionary precursor of more complex forms of predation—has modelled the conceptual framework of modern hunter-gatherers, what might be the potential evolutionary consequences of relationships with animals with higher body mass for the Order Primates? A glimpse into the different modes and intensities of relations with vertebrate prey among living non-human primates may help reconstruct archaic patterns of animal-hominin interactions and forms of embodiment and cognition that paved the way for higher-order relational processes.

3.2. *Vertebrate predation among non-human primates*

It is reasonable to believe that the ancient socio-cognitive faculties and bioecological factors essential for the carnivorous behaviour of the primate order lie within a dynamic evolutionary framework. Nevertheless, these behavioural and cognitive traits are unevenly distributed among primate taxa and likely denote species-specific adaptive and trophic niches. If, according to empirical evidence, approximately 89 primates incorporate animal matter in their diets (Watts, 2020), then variations in meat-eating behaviour are likely to be expected within and between species. These behavioural variations thus show the intensity of predator-prey interactions, namely, the degree of primates' bodily exposure and socio-cognitive engagement with vertebrate prey.

In this context, low-level, opportunistic, and somewhat fortuitous carnivory has been reported among various primates, e.g., snub-nosed monkeys (*Rhinopithecus* spp.*:* Zhao et al., 2008; Ren et al., 2010), guenons (*Cercopithecus:* Butynski, 1982a; Fairgrieve, 1997; Tapanes et al., 2016; Lile et al., 2020), grey-cheeked mangabeys *(Lophocebus albigena:* Poulsen and Clark, 2001), mandrills (*Mandrillus sphinx*: Kudo and Mitani, 1985), Japanese macaques (*Macacafuscata yakui:* Suzuki et al.,

1990) black crested gibbons (*Nomascus concolor jingdongensis:* Fan and Jiang, 2009) and Orangutans (*Pongo* spp.*:* Sugardjito and Nurhuda, 1981; Utami and van Hooff, 1997; Hardus et al., 2012; Buckley et al., 2015). At the opposite end of the spectrum, an apparent more regular predatory and meat-eating behaviour (high-level carnivory) has been observed in Cebidae, e.g., white-faced capuchin monkeys (*Cebus capucinus:* Fedigan, 1990; Perry and Rose, 1994; Rose, 1997) and bearded capuchin monkeys (*Sapajus libidinosus:* Falótico et al., 2018; Filho et al., 2021; Falótico, 2023); in baboons (*Papio* spp.), e.g., grey-footed chacma baboons (*Papio ursinus griseipes:* Allan et al., 2022), olive baboons (*Papio anubis:* Strum, 1975; Sommer et al., 2016), Guinea baboons (*Papio*: Goffe and Fischer, 2016), yellow baboons (*Papio cynocephalus*: Hausfater, 1976; Rhine et al., 1986), and hamadryas baboons (*Papio hamadryas:* Schreier et al., 2019); and finally in our closest living relatives chimpanzees (*Pan troglodytes:* Stanford, 1995; Pruetz and Bertolani, 2007; Fahy et al., 2013; Gilby and Wawrzyniak, 2018) and bonobos (*Pan paniscus*: Hohmann and Fruth, 2007; Surbeck and Hohmann, 2008; Surbeck et al., 2009; Wakefield et al., 2019).

At a rudimentary level of socio-ecological niches and multispecies relationalities, the consumption of vertebrate prey that occurs in a wide array of primate taxa (from monkeys to great apes) points to patterns of predation (the degree and modes of modification and assimilation of animal tissues) that may have irregularly evolved in this order. If ancient ecological constraints were pivotal in the evolution of primates' body plan and hence the emergence of carnivory (Wu et al., 2022), it might be postulated that differences in predatory and meat-eating behaviour in extant primates stem from behavioural adjustments to particular ecological conditions. This thus entails the prominence of foraging and feeding patterns in modulating primate cognitive complexity, underlining the positive correlation between a high-quality diet and brain size (DeCasien et al., 2017).

It then follows that, instead of social complexity (group size and maintenance of social relations) as a principal factor of primates' increased brain/neocortex size (Dunbar, 1998), the different modalities and degrees of animal matter acquisition, modification, and incorporation were primary drivers of social and cognitive evolution. Haplorhines, for example, exhibit enhanced visual areas, large brains, and high-quality diets (Barton, 1998), indicating that selection on sensory and cognitive specialisations not only developed in response to divergent socio-ecological niches (DeCasien and Higham, 2019) but likely emerged (as in the case of carnivory) from highly embodied engagements with living matter (interspecies intersections and exchanges of essential bodily compounds), laying the foundations for social-cognitive systems complexification. Nevertheless, even though both ecology and sociality may have affected (albeit to different degrees in different clades) primate brain-size variation, highlighting the diverging evolutionary history of each taxon (Grabowski et al., 2023: 416), the adaptation and level of engagement with specific trophic niches may have had significant implications for primates' socio-cognitive evolution. More explicitly, the variation in predatory and meat-eating behaviour in living primates has likely depended on unique phenomenal qualities (intended here as intra- and interspecific variations in the adaptation and degree of bodily and cognitive engagement with organic and inorganic agents), which, being part and parcel of particular relational processes, may thus have paved the way for potential evolutionary changes in morphological, behavioural, and cognitive patterns.

3.3. Disentangling elements of primate predatory behaviour

Because vertebrate consumption relies upon the interweavings of primates, sympatric species (from apex predators to prey), and the physical environment, the analysis must be restricted to specific modalities of predation and meat-eating patterns to delineate likely primary socio-cognitive configurations. These are therefore exemplified by a suite of cognitive and behavioural traits, as well as the degree and intensity of bodily contact with prey animals. For example, these traits are mainly encompassed by (*i*) forms of prosociality related to prey acquisition, such as social tolerance, social and cooperative hunting and meat sharing (whether in its passive and active forms); (*i*) technological skills such as the use of tools to hunt/catch prey (e.g., tool-assisted hunting, tool-assisted fish catching); and (*iii*) both passive and confrontational scavenging behaviour. For clarification purposes, definitions of the aforementioned key terms discussed throughout the text are given in Table 1.

The comparison of these species-specific traits must hence show (a) whether elementary forms of cognition and prosocial behaviour (e.g., tool-assisted predation, meat sharing, hunting and/or scavenging patterns) could represent precursors of hominin carnivory and (b) the potential evolutionary significance of primate socio-ecology and cognitive architecture as the basis for the development of more complex forms of thinking in the hominin lineage.

3.4. *"Low levels" of predation and forms of meat-eating behaviour among extant primates*

The evolutionary roots of animals' morphological and cognitive complexity (likely associated with the events of the Cambrian period, ~540 Mya) may have had profound implications for the predatory behaviour of extant taxa (Trestman, 2013). Primate carnivory may then be a particular ramification of the most elementary behavioural and cognitive qualities shared by the animal kingdom. These are, in other words, the agential capabilities of organisms to adapt, modify, and especially relate to ecological niches. It is at the nexus of modification and assimilation of biological elements and the degree to which organisms are immersed in trophic interactions that a given pattern of predation emerges. Accordingly, and as demonstrated by the variation in meat-eating behaviour among the Primate order, different socio-ecological and cognitive factors (e.g., prey [type, size, and density], the intensity of predator-prey interactions, level of intraspecific sociality, and tool use) have likely modulated the diverse evolutionary pathways of species' dietary patterns. Within this framework, remarkable variations are to be found at the most basic level of ecological

Table 1
Definitions of main behavioural traits used in the study.

Behavioural trait	Definition
Social tolerance	A nonaggressive interaction between conspecifics during predation and/or meat consumption events.
Social hunting	A predation instance characterised by social interactions between conspecifics without involving any form of coordination and cooperation in the hunt.
Cooperative hunting	An instance of predation in which two or more animals show coordinated actions and cooperative behaviour for the acquisition of prey.
Passive meat sharing	An animal takes meat from the vicinity of a carcass owned by a conspecific without any form of aggression exhibited by the latter.
Active meat sharing	A direct transfer of meat from an animal to other conspecific individuals.
Tool-assisted hunting	The use of tools to hunt terrestrial vertebrates.
Tool-assisted fish catching	The use of tools to catch fish.
Tool-assisted carcass processing	The use of tools aimed at accessing animal tissues from a carcass. Although extremely rare among primates, most occurrences involve the use of percussive proto-tools (e.g., smashing skulls against tree trunks).
Passive scavenging	Consumption of a carcass in the absence of its predator or other powerful scavengers (Mateos et al., 2025).
Confrontational scavenging	Is a form of scavenging behaviour (also known as active/power scavenging) where consumption of carrion entails the confrontation and subsequent displacement of a predator or scavenger from the carcass site (Mateos et al., 2025). Note that, for the sake of simplicity, the terms "confrontational scavenging" and "kleptoparasitism" are used here interchangeably (but see Mateos et al., 2025, for a different definition of the two terms).

relations with prey taxa that may then determine the stimulation of potential socio-cognitive mechanisms that would enhance the continuity and intensity of trophic exchanges. Hence, the fundamental and species-specific traits of carnivory may be approached by looking closely at the modes and degree of relation, modification, and assimilation of vertebrate tissues (see Tables 2 and 3 for further details).

As mentioned, some primates' hunting and meat-eating behaviour patterns are highly opportunistic; thereby, predator-prey intersections may reflect a minimum socio-material intensity. This predatory pattern of behaviour is exhibited amongst several guenon species. For instance, for blue monkeys (*Cercopithecus mitis stuhlmanni*), Butynski (1982a) reported two cases of predation on galagos (henceforth bushbabies) (*Galago demidovi/Galago senegalensis*), Fairgrieve (1997), one on a flying squirrel (*Anomalurus derbianus jacksonii*), Wahome et al. (1988) various potential instances of predation on mice, and Akankwasa et al. (2020) an intriguing case of predation on an infant guereza colobus monkey (*Colobus guereza occidentalis*); for red-tailed monkeys (*Cercopithecus ascanius*), Furuichi (2006) observed two successful cases of predation on green pigeons (*Treron calva*), and Lile et al. (2020) one on a white-crested helmetshrike (*Prionops plumatus*); and, lastly, for vervet monkeys (*Cercopithecus aethiops*), Struhsaker (1967) reported three instances of feeding on yellow-necked spurfowl chicks (*Pternistis leucoscepus*).

Rare cases of predation have also been observed on bay duikers (*Cephalophus dorsalis*) by mandrills (*Mandrillus sphinx*: Kudo and Mitani, 1985); on squirrels (*Funisciurus* sp.) and bushbabies (*Galago alleni*) by grey-cheeked mangabeys *(Lophocebus albigena:* Poulsen and Clark, 2001); on swinhoe's striped squirrel (*Tamiops swinhoei*) and several bird species (*Garrulus landarius*, *Dryocopus javensis*, *Milvus migrans*, *Urocissa erythrorhyncha*) by snub-nosed monkeys (*Rhinopithecus bieti*: Ren et al., 2010); on frogs (*Rana tagoi yakushimaensis* and *Hyla japonica*), lizards (*Eumeces latiscutatus* and *Gekko yakuensis*) and brown trout (*Salmo trutta*) by Japanese macaques (*Macacafuscata yakui*; Suzuki et al., 1990; Milner et al., 2021); and on giant flying squirrels (*Petaurista philippensis*) by black crested gibbons (*Nomascus concolor jingdongensis*: Fan and Jiang, 2009).

Likewise, amongst callitrichines, behavioural observations indicate occasional instances of predation by moustached tamarins (*Saguinus mystax*), black lion tamarins (*Leontopithecus chrysopygus*), saddle-back tamarins (*Saguinus fuscicollis*), and common marmosets (*Callithrix jacchus*) on anurans (family Hylidae including species with toxic skin secretions) and reptiles (family Iguanidae, Teiidae, Scincidae, and Polychrotidae) (Heymann et al., 2000; Beltrão-Mendes et al., 2018; Lüffe et al., 2018; Garbino et al., 2020); and by black-tufted-ear marmosets (*Callithrix penicillata*) on agile opossums (*Gracilinanus agilis*; de Camargo et al., 2017). Orangutans (*Pongo* spp.) also display similar sporadic and opportunistic feeding patterns. For example, two potential occurrences of scavenging have been reported so far: one involving a young female Sumatran orangutan (*Pongo abelii*) feeding on a gibbon[1] (*Hylobates lar*; Sugardjito and Nurhuda, 1981) carcass, and another an adult flanged male Bornean orangutan (*Pongo pygmaeus*; Buckley et al., 2015) eating a horse-tailed squirrel (*Sundasciurus hippurus*) carcass. In addition to these isolated scavenging incidents, a few occurrences of predation on slow lorises (*Nycticebus coucang* and *Nycticebus borneanus*) have been reported by Sumatran orangutans (*Pongo abelii*) at the research sites of Ketambe (Utami and van Hooff, 1997; Hardus et al., 2012) and Suaq Balimbing (van Schaik et al., 2003), Northern Sumatra; and by Bornean orangutans (*Pongo pygmaeus*) at the Tuanan Orangutan Research Station, Central Kalimantan (Makur et al., 2022). Russon et al. (2014) also reported that rehabilitant Bornean orangutans (*Pongo pygmaeus*) living on three forested islands in Central Kalimantan feed on dead and live fish (e.g., *Kryptopterus*, *Ompok*, and *Channa* spp.).

Interestingly, the analogous patterns of meat-eating behaviour frequency, predator-prey body size relationships, and the degree of socio-material intensity (from meat sharing to tool-assisted predation) involved in trophic interactions exhibited by these primate species may suggest a rudimentary form of carnivory (Table 2). Nevertheless, even though these behavioural patterns likely evolved from specific ecological pressures, such as seasonal food shortages (Wahome et al., 1988; Fairgrieve, 1997; Hardus et al., 2012; Buckley et al., 2015), even the consumption of scraps of vertebrate matter (e.g., squirrels, *Funisciurus* sp., and bushbabies, *Galago alleni* by grey-cheeked mangabeys, *Lophocebus albigena*: Poulsen and Clark, 2001; or anurans by Japanese macaques, *Macacafuscata yakui*: Suzuki et al., 1990) might provide not only macronutrients but also essential micronutrient elements nearly absent in plants (Tennie et al., 2009; Watts, 2020; Lima and Bicca-Marques, 2024).

The lines of evidence from Table 2 indicate that (1) meat sharing is almost absent in the carnivorous feeding behaviour of these primate taxa with the only exception of black crested gibbons, *Nomascus concolor jingdongensis* (Fan and Jiang, 2009), Sichuan snub-nosed monkeys, *Rhinopithecus roxellana* (Zhao et al., 2008) and Sumatran orangutans, *Pongo abelii* (Utami and van Hooff, 1997; Hardus et al., 2012) who show primarily passive meat sharing patterns; (2) hunting behaviour is highly opportunistic and individualistic, showing mainly agonistic intraspecific patterns (but see for mandrills, *Mandrillus sphinx*; Kudo and Mitani, 1985; and for black crested gibbons, *Nomascus concolor jingdongensis*; Fan and Jiang, 2009); consequently, there appears to be little room for cooperation in vertebrate predation; (3) scavenging appears to be rare and has been only reported in its passive form in Bornean orangutans (*Pongo pygmaeus*: Buckley et al., 2015), snub-nosed monkeys (*Rhinopithecus bieti*: Ren et al., 2010) and probably in Sumatran orangutans (*Pongo abelii*: Sugardjito and Nurhuda, 1981) although this incident has been objected (Meijaard, 1999; Hardus et al., 2012); and (4) except for Bornean orangutans (*Pongo pygmaeus*) who attempt to catch fish using stick tools (Russon et al., 2014), no records of tool-assisted predation have been documented so far.

Though these non-human primates' low-level predatory and meat-eating behaviour might appear on the surface as weak referential models for the evolution of hominin carnivory, these species' underlying behavioural and cognitive mechanisms are worth exploring. So, the somewhat rudimentary behavioural qualities exhibited in meat-eating strategies may indicate a set of combinations of ancestral cognitive capabilities lost or otherwise differently evolved (Bruner, 2024) throughout the evolution of the hominin lineage. It seems therefore likely that phenotypic plasticity played a key role in the change of certain cognitive abilities shared by the earliest primates. The common ancestor of living primates, which exhibited specific morphological and cognitive traits fundamental for ambush predation (Wu et al., 2022), is just an example of how its behavioural repertoire could have developed into ramifications and further amalgamations of the ancient feeding pattern. This basal neurocognitive structure would thus have allowed the development of behaviour patterns unique to each taxon but contingent on particular socio-ecological conditions. By this logic, one may point to the fact that beneath the rare occurrences of vertebrate consumption by these primates, there are probably cognitive qualities of significant importance to the potential reconstruction of ancient predatory and meat-eating behaviour patterns.

Therefore, the distinctive prosocial behaviour (i.e., intraspecific social tolerance during vertebrate predation and meat sharing patterns) exhibited by mandrills, *Mandrillus sphinx* (Kudo and Mitani, 1985), black crested gibbons, *Nomascus concolor jingdongensis* (Fan and Jiang, 2009), Sichuan snub-nosed monkeys, *Rhinopithecus roxellana* (Zhao et al., 2008), and Sumatran orangutans, *Pongo abelii* (Utami and van Hooff, 1997; Hardus et al., 2012); the unusual instances of scavenging amongst primates showed by Bornean orangutans, *Pongo pygmaeus* (Buckley et al., 2015), snub-nosed monkeys, *Rhinopithecus bieti* (Ren

[1] It is important to note, however, that according to Rijksen and Meijaard (1999) and Hardus et al. (2012), this potential scavenging incident was likely a case of hunting of a slow loris by the orangutan.

Table 2
Traits of the meat-eating behaviour of primates of low-level carnivory.

Genus	Species	Site	Ecosystem	Prey type	Cognitive skill(s)/behaviour pattern(s)	Source(s)
Pongo	Bornean orangutans (*Pongo pygmaeus*)	Central Kalimantan (Indonesia)	Forest	Fish (unidentified species of walking fish)	**Tool-assisted fish catching** A female orangutan attempted to catch fish by jabbing a sturdy branch into a shallow pond.	Russon et al. (2014)
	Sumatran orangutans, (*Pongo abelii*)	Ketambe (Indonesia)	Forest	Slow loris (*Nycticebus spp.*)	**Meat sharing** A female orangutan shared meat passively with her 5-year-old son.	Utami and van Hooff (1997)
				Slow loris (*Nycticebus coucang*)	**Meat sharing/prey detection ability?** Sequences of passive meat transfer were observed between a mother-infant dyad; the orangutan may have used olfactory cues to detect the prey.	Hardus et al. (2012)
		Gunung Leuser (Indonesia)	Forest	Gibbon (*Hylobates lar*)	**Passive scavenging?** A likely case of a female orangutan scavenging on a gibbon carcass; other researchers have regarded the incident as a potential orangutan consumption of a slow loris.	Sugardjito and Nurhuda (1981); but see Rijksen and Meijaard (1999); Hardus et al. (2012)
	Bornean orangutans (*Pongo pygmaeus*)	Central Kalimantan (Indonesia)	Forest	Horse-tailed squirrel (*Sundasciurus hippurus*)	**Passive scavenging** An adult flanged male orangutan was observed feeding on a horse-tailed squirrel carcass, likely found in the trees.	Buckley et al. (2015)
Nomascus	Black crested gibbons (*Nomascus concolor jingdongensis*)	Yunnan (China)	Forest	Giant flying squirrel (*Petaurista philippensis*)	**Meat sharing/social tolerance** Instances of predation on giant flying squirrels (primarily by a female) involved passive meat transfer between group members; the two reproductive females involved in the sharing event also displayed a high degree of tolerance.	Fan and Jiang (2009)
Mandrillus	Mandrills (*Mandrillus sphinx*)	Campo Ma'an (Cameroon)	Forest	Bay duiker (*Cephalophus dorsalis*)	**Social tolerance** A relationship of tolerance was reported between an adult male and an adult female mandrill during predation on a bay duiker; no aggressive interactions were observed in the hunting episode.	Kudo and Mitani (1985)
Rhinopithecus	Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*)	Qinling Mountains (China)	Forest	Eurasian blackbird (*Turdus merula*)	**Meat sharing** An instance of passive meat sharing occurred when an adult male transferred to an adult female an Eurasian blackbird's thigh previously hunted by the former.	Zhao et al. (2008)
	Snub-nosed monkeys (*Rhinopithecus bieti*)	Yunnan (China)	Forest	Red-billed blue magpie (*Urocissa erythroryncha*)	**Passive scavenging** A young female was seen eating a frozen, red-billed blue magpie carcass, probably killed by the heavy snow.	Ren et al. (2010)

et al., 2010) and perhaps Sumatran orangutans (*Pongo abelii*: Sugardjito and Nurhuda, 1981); the potential use of olfactory cues by Sumatran orangutans (*Pongo abelii*) to locate slow lorises (Hardus et al., 2012); and the rare tool-using behaviour (i.e., the manipulation of organic matter like sticks used to catch fish) by Bornean orangutans, *Pongo pygmaeus* (Russon et al., 2014), may indicate primary forms of behaviour and socio-cognitive capacities that, irrespective of the phylogeny, ontogeny, and independent specialisation of each taxon, should have opened the way for the exploration and penetration into novel trophic levels and the further maximization of the carnivorous niche.

Such a process likely occurred gradually, largely because of the nature of primate carnivory and its heavy reliance on intra-specific/inter-specific relationalities (i.e., cooperative hunting/scavenging and predator-prey interactions) and the intensity of sensible qualities involved in the modification, assimilation, and compenetration of organic and inorganic matter (i.e., consumption/predation of vertebrate prey and manipulation of wooden and stone tools). Following this line of reasoning, higher levels of meat-eating behaviour should be examined in other primate species to provide more nuanced referential templates for the potential reconstruction of the evolution of hominin carnivory.

3.5. *"High levels" of predation and forms of meat-eating behaviour among extant primates*

As noted above, amongst non-human primates, vertebrate predation seems to be of a higher degree in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), baboons (*Papio* spp.), and Cebines of the genus *Cebus* and *Sapajus* spp. (Watts, 2020). Compared with the species of low-level carnivory, it might be argued that these primates' higher-level meat-eating behaviour is probably the empirical corroboration of the hypothetical feeding patterns of ancient hominins. However, could a high degree of meat-eating behaviour in extant primates be fundamental to revealing structural commonalities with archaic hominins and even modern hunter-gatherers? If so, what would be the most critical cognitive attributes to constructing strong conjectures about the evolutionary trajectories of these subsistence strategies? As with primates of low-level carnivory, a cogent starting point may be the behaviour patterns and embodied cognition exhibited by primates of higher-level carnivory (Table 3).

Comparing the empirical realities of primates of both low-level and high-level carnivory (Tables 2 and 3), an interesting evolutionary picture emerges from varied feeding patterns that likely show elementary socio-cognitive qualities. This underlying ancient structure must have nevertheless been highly exposed to a wide range of selection pressures that modelled particular forms of meat-eating behaviour patterns. Extant primates, then, likely exhibit a patchy amalgamation of behavioural and cognitive processes substantially dependent on environmental, ecological, and social factors. By extension, the different degrees of primates' behavioural plasticity minimally required to respond to specific environmental inputs enabled them to move into a higher trophic level; feeding on vertebrate matter was thus likely the evolutionary cause and effect of adaptive behaviours and their various ramifications. Even if the primary significance of primate carnivory is likely to be the dietary supplementation of micronutrients lacking in the vegetal world

Table 3
Traits of the meat-eating behaviour of primates of high-level carnivory.

Genus	Species	Site	Ecosystem	Prey type	Cognitive skill(s)/behaviour pattern(s)	Source(s)
Pan	Chimpanzees (*Pan troglodytes*)	Fongoli (Senegal)	Savanna	Bushbabies *(Galago senegalensis)*	**Tool-assisted hunting** A complex modification of branches (by trimming) to construct spearing tools was primarily exhibited by females and immature chimpanzees to prey on bushbabies hidden in cavities of hollow branches or trees.	Pruetz and Bertolani (2007)
		Mahale (Tanzania)	Forest	Giant forest squirrel (*Protoxerus stangeri*?) or red-legged sun squirrel (*Heliosciurus rufobrachium*?)	**Tool-assisted hunting/meat sharing** A female orphan chimpanzee preyed on a squirrel hidden in a tree's hole (*Albizia glaberrima* (Schumach. & Thonn.) Benth.) using a modified branch (probing into a hole and then rousing the animal) of the same tree; bouts of meat sharing with another female orphan ensued from the predation event.	Huffman and Kalunde (1993)
				Red-legged sun squirrel *(Heliosciurus rufobrachium)* Yellow-spotted rock hyrax (*Heterohyrax Brucei?*)	**Tool-assisted hunting** The first (successful) tool-using behaviour occurrence involved a female using a stick (probably as a weapon that killed or severely injured the prey) to poke into a tree hollow to hunt a squirrel; in the second instance, a likely predation attempt on hyrax hidden in a cave (a possible nesting place) by six males included the use of different plant matter (e.g., *Cissus oliveri* and *Psychotria Peduncularis*) as rousing tools and even weapons.	Nakamura and Itoh (2008)
		Batan (Senegal)	Savanna	Bushbabies (*Galago senegalensis*?)	**Tool-assisted hunting?** Two alleged hunting tools (*Cordyla pinnata* sticks) were found near potential bushbabies' nesting cavities.*Cordyla*	Micheletti et al. (2022)
		Moukalaba (Gabon)	Forest	Medium-sized mammal (probably an unknown species of mongoose)	**Cooperative tool-assisted hunting?** Two adult male chimpanzees likely used two different sticks of *Afrostyrax lepidophyllus* (sapling) in an apparent act of cooperative predation: one to pound and enlarge the crack of a fallen log *Afrostyrax lepidophyllus* (likely to chase a prey) and the other to drive out and ambush the prey (possibly an unidentified mongoose species) hidden in the log.	Wilfried and Yamagiwa (2014)
		Ndoki (Republic of Congo)	Forest	Hornbill (?*Ceratogymna* sp.) Crowned guenon (*Cercopithecus pogonias*)	**Meat sharing/attempt of tool-assisted hunting?** All instances of predation involved passive meat sharing between adults, juveniles, and infants of both sexes; also, an adult female poked a large dead branch into a hole, likely attempting to prey upon a hornbill (*Ceratogymna sp.*).	Kuroda et al. (1996)
		Taï (Côte d'Ivoire)	Forest	Mainly red colobus (*Piliocolobus badius*)	**Tool-assisted carcass processing/ percussive proto-tool use/ cooperative hunting/meat sharing** Besides the high levels of cooperative hunting and meat-sharing, chimpanzees used fashioned small sticks to extract marrow from bones previously broken by their teeth; they also opened the monkeys' skulls by banging them against a tree trunk or a root.	Boesch and Boesch (1989)
				Mainly red colobus (*Piliocolobus badius*)	**Cooperative hunting/meat sharing** Chimpanzees exhibited complex patterns of cooperative behaviour and coordination; the higher the cooperation (number of hunters) in hunting, the more likely an increase in hunting success and meat sharing.	Samuni et al. (2018)
		Rekambo (Gabon)	Forest	Hinge-back tortoises (*Kinixys erosa*)	**Percussive proto-tool use/meat sharing/food storage?** Predation on hinge-back tortoises by adult males involved smashing the plastron with one hand against a wooden	Pika et al. (2019)

(*continued on next page*)

Table 3 (*continued*)

Genus	Species	Site	Ecosystem	Prey type	Cognitive skill(s)/behaviour pattern(s)	Source(s)
					anvil (e.g., trunk), which, in most cases, resulted in peaceful and cooperative food sharing among members; also, after consuming roughly half of the tortoise meat, an alpha male was observed clamping the remaining parts of the carcass into a tree fork to subsequently retrieve the following day.	
		Issa (Tanzania)	Savanna	Bushbuck (*Tragelaphus scriptus*)	**Confrontational scavenging/ kleptoparasitism** An adult male chased off a crowned eagle, *Stephanoaetus coronatus,* gaining access to the carcass, which he and three other chimpanzees further consumed.	Baker et al. (2024)
		Mahale (Tanzania)	Forest	Blue duiker (*Philantomba monticola)*	**Confrontational scavenging/ kleptoparasitism** Chimpanzees obtained a freshly killed animal from a leopard, *Panthera pardus;* notwithstanding the predator in the vicinity (they were observed emitting waa barks), they proceeded to scavenge the carcass.	Nakamura et al. (2019)
				Blue duiker (*Philantomba monticola)*	**Confrontational scavenging/ kleptoparasitism** A male stole a blue duiker kill from a small ambush predator (likely an African civet, *Civettictis civetta,* or ratel, *Mellivora capensis*?); he then scavenged meat around the head and discarded the entire body.	Hosaka and Ihobe (2015)
				Blue duiker (*Philantomba monticola)* Bushbuck (*Tragelaphus scriptus*)	**Passive/confrontational scavenging?** Four episodes of scavenging were recorded as follows: the first involved a group of chimpanzees who eagerly ate a non-fresh blue duiker carcass (it possibly had died of disease or shock) provided by humans; in the second instance, chimpanzees also excitedly consumed a freshly killed blue duiker (likely killed by a leopard, *Panthera pardus* or serval, *Leptailurus serval*) provided by humans; in the third chimpanzees scavenged on a bushbuck carcass likely left over by a leopard or usurped from it; and in the fourth, chimpanzees were observed gnawing on parts of a nearly defleshed bushbuck carcass (likely killed and cached by a leopard).	Hasegawa et al. (1983)
				Red colobus (*Procolobus tephrosceles*)	**Confrontational scavenging/ kleptoparasitism?** A potential occurrence in which chimpanzees appropriated a carcass from a leopard, *Panthera pardus*.	Hosaka (2015)
				Bushbuck (*Tragelaphus scriptus*)	**Passive scavenging** Six chimpanzees found a fresh kill bushbuck that had been recently left on the ground by a leopard, *Panthera pardus*; they then started feeding on it noiselessly.	Hosaka et al., 2001
		Gombe (Tanzania)	Forest	Bushbuck (*Tragelaphus scriptus*) Helmeted Guinea Fowl (*Numida meleagris*)	**Confrontational scavenging/ kleptoparasitism** Several instances of interspecific competition for meat were reported; in these incidents, chimpanzees appropriated carcases from olive baboons (*Papio anubis*).	Morris and Goodall (1977)
				Bushbuck (*Tragelaphus scriptus*)	**Passive scavenging** A case of scavenging on a carcass recently killed by a leopard, *Panthera pardus*; note that only a few juveniles ate small amounts of meat, while the other chimpanzees, although curious, were not interested in consuming the carcass.	Muller et al. (1995)
		Ngogo (Uganda)	Forest	Red duiker (*Cephalophus monticola*) Red colobus (*Procolobus tephrosceles*) Red-	**Passive scavenging** Chimpanzees appeared to have scavenged on four occasions: in the first, they ate small amounts of meat from a	Watts (2008)

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Table 3 (*continued*)

Genus	Species	Site	Ecosystem	Prey type	Cognitive skill(s)/behaviour pattern(s)	Source(s)
				tailed monkey (*Cercopithecus ascanius*)	dead adult female red duiker; in the second, they consumed and shared the meat of a red colobus carcass likely killed by another chimpanzee the previous day; in the third, a young adult male scavenged on a dead subadult male red-tailed monkey likely killed by a crowned eagle, *Stephanoaetus coronatus*; in the fourth, chimpanzees fed on and fought over (though occasionally sharing the carcass) the meat of a freshly killed subadult red duiker (likely killed by a crowned eagle).	
	Bonobos (*Pan paniscus*)	LuiKotale (Democratic Republic of the Congo)	Forest	Peter's duiker (*Cephalophus callipygus*)	**Meat sharing/social tolerance** An alpha male of the W community caught and shared the meat of a duiker with females of his community and females with the E community; bonobos' intercommunity social tolerance also involved the peaceful transfer of meat between females of both communities and their offspring.	Fruth and Hohmann, 2018
				Wolf's guenon (*Cercopithecus wolfi*) Redtail monkey (*Cercopithecus ascanius*)	**Meat sharing/prey detection ability** The carcass's possessors were observed to transfer pieces of meat to other group members actively; bonobos used auditory and visual cues to detect prey.	Surbeck and Hohmann (2008)
		Wamba (Democratic Republic of the Congo)	Forest	Scaly-tailed squirrel (*Anomalurus* sp.)	**Meat sharing** Incident of passive and active meat transfer between two females with dependent offspring; despite displaying non-aggressive behaviour, the possessor occasionally exhibited mild rejection towards the beggar, apparently only sharing the less valuable parts of the carcass.	Hirata et al. (2010)
				Scaly-tailed squirrel (*Anomalurus* sp.)	**Meat sharing** Two occurrences of meat-eating and meat-sharing behaviour between adult females and between mother and infant were observed.	Tashiro (2001)
		Kokolopori (Democratic Republic of the Congo)	Forest	Duiker (*Cephalophus* spp.) Scaly-tailed squirrel (*Anomalurus* sp.) African striped squirrel (*Funisciurus* sp.)	**Meat sharing/potential cultural determinants underpinning the diversity of predatory patterns of two bonobo groups?** Regardless of local ecology, group-specific prey acquisition patterns may have emerged from culturally transmitted hunting skills, allowing particular forms of social tolerance and reciprocal exchanges between neighbouring groups occupying diverse trophic niches.	Samuni et al. (2020)
		Lomako (Democratic Republic of the Congo)	Forest	Unidentified mammal (the size of a large squirrel?) Duiker (*Cephalophus* spp.)	**Meat sharing** Two cases of meat-sharing involving relaxed interactions between several individuals (principally females) and infants were reported.	Hohmann and Fruth (1993)
				Mainly weyn's duiker (*Cephalophus weynsi*)	**Meat sharing** Instances of meat-eating and sharing ranged from peaceful to aggressive interactions; notably, most predation events involved female control of the carcass, aggressive behaviour towards male beggars, and meat transfer between females.	Wakefield et al. (2019)
		LuiKotale (Democratic Republic of the Congo)	Forest	Black-crested Mangabey (*Lophocebus aterrimus*)	**Confrontational scavenging/ kleptoparasitism ?** A potential case of carcass theft from predators, such as crowned eagle (*Stepahnoaetus coronatus*), golden cat (*Felis aurata*), or leopard (*Panthera pardus*) might be inferred from indirect evidence of bonobo meat-eating behaviour (i.e., a faecal sample containing the digit of an immature black mangabey and a pelt of a black	Surbeck et al. (2009)

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Table 3 (*continued*)

Genus	Species	Site	Ecosystem	Prey type	Cognitive skill(s)/behaviour pattern(s)	Source(s)
					mangabey found near the faecal sample).	
Papio	Chacma baboons (*Papio ursinus*)	Namib Desert (Namibia)	Desert	Mozambique tilapia (*Oreochromis mossambicus*) Common carp (*Cyprinus carpio*) Chubbyhead barb (*Enteromius anoplus*)	**Tool-assisted fish catching** The use of sand to subdue active live fish was observed among chacma baboons' high-ranking adult males and lower-ranking individuals; the first carried fish away from pools and then dropped them onto river bars and piled dry sand on them, whereas the second brushed fish on the sand as they retreated from pools to avoid higher-ranking individuals.	Hamilton and Tilson (1985)
	Olive baboons (*Papio anubis*)	Gilgil (Kenya)	Savanna	Thomson's gazelle (*Eudorcas thomsonii*) Cape hare (*Lepus capensis*) Dik-dik (*Rhyncotragus kirki*) Steinbok (*Raphicerus campestris*) Impala (*Aepyceros melampus*)	**Cooperative hunting/meat sharing** Olive baboons developed a rudimentary cooperative technique to hunt more successfully than the individual hunt; likewise, rudimentary forms of meat transfer were either deployed by individuals (who aggressively displaced each other for the carcass) or by sharing between a female and her offspring or between an adult male and an adult female.	Strum (1975)
	Guinea baboons (*Papio*)	Niokolo-Koba (Senegal)	Savanna	Bushbuck (*Tragelaphus scriptus*) African savanna hare (*Lepus microtis*)	**Meat sharing/social tolerance** Passive meat sharing was only observed between males and females of the same social and reproductive units; this tolerated food transfer occurred irrespective of female sexual receptivity.	Goffe and Fischer (2016)
				Bushbuck (*Tragelaphus scriptus*)	**Meat sharing/social tolerance** Passive transfers of meat characterised by tolerant behaviour were exhibited by the multi-level society of Guinea baboons; these were modulated by the quality of social relationships and gradients of familiarity within social levels between dyads.	O'Hearn et al. (2025)
	Yellow baboons (*Papio cynocephalus*)	Amboseli (Kenya)	Savanna	Gazella sp.	**Passive scavenging?** A gazelle's detached shoulder and foreleg were carried and chewed by an adult male (no blood stains were noted in his fur, and no other animal parts could be located), prompting other individuals to consume the leg; in another instance, several adult males fought over and fed from the detached head and neck of an adult gazelle.	Hausfater (1976)
	Grey-footed chacma baboons (*Papio ursinus griseipes*)	Mashatu (Botswana)	Savanna	Helmeted Guinea Fowl (*Numida meleagris*)	**Confrontational scavenging/ kleptoparasitism** An adult male stole the body of an adult guinea fowl freshly killed by a Tawny Eagle, *Aquila rapax* (the predator was eating the head and neck of the fowl whilst its body fell on the ground being then grabbed by the baboon); an unsuccessful attempt from the Tawny Eagle to regain the carcass and the competition between baboons and Black-backed jackals (*Canis mesomelas*) for a discarded fowl's wing followed the scavenging episode.	Branch (2017)
		Soutpansberg (South Africa)	Forest	Bushbuck (*Tragelaphus scriptus*)	**Passive scavenging?** An adolescent male was observed climbing into a tree and coming back to the ground with a bushbuck corpse (larger than the commonly hunted animals), likely killed and cached by a leopard (*Panthera pardus*).	Allan et al. (2022)
	Chacma baboons (*Papio ursinus*)	Tswalu (South Africa)	Savanna	Springbok (*Antidorcas marsupialis*)	**Confrontational scavenging/ kleptoparasitism** A troop of between 30 and 40 chacma baboons were observed stealing a springbok kill from a female cheetah (*Acinonyx jubatus*); though no observations were recorded (due to observer distance) of the baboons	Davis et al. (2024)

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Table 3 (*continued*)

Genus	Species	Site	Ecosystem	Prey type	Cognitive skill(s)/behaviour pattern(s)	Source(s)
					feeding on the carcass, the baboons' proximity to the springbok suggests that they likely did it.	
		Hluhluwe–Imfolozi (South Africa)	Savanna	Impala (*Aepyceros melampus*)	**Confrontational scavenging/ kleptoparasitism** While a male cheetah (*Acinonyx jubatus*) was eating a recently killed sub-adult female impala; a troop of ~20 chacma baboons chased the cheetah off from the kill, and one adult male baboon began to consume the carcass.	Davis et al. (2024)
Sapajus	Bearded capuchins (*Sapajus libidinosus*)	Serra da Capivara (Brazil)	Savanna	*Tropidurus* ssp.	**Tool-assisted hunting/meat sharing** Probe tool use (mostly small branches modified by trimming) was observed among bearded capuchin monkeys to enhance predation upon lizards by expelling them from rock crevices; although rare, meat sharing was observed primarily between males.	Falótico and Ottoni (2014); Falótico (2023)
				Rocky cavy (*Kerodon rupestris*)	**Tool-assisted hunting** Bearded capuchins were observed attempting to dislodge rock cavies (large prey relative to their body size) from hiding places using longer spear-like tools.	Falótico (2023)
	Brown/tufted capuchins (*Sapajus apella*) (formerly *Cebus apella*)	Parque Zoológico de Goiânia (Brazil)	Artificial setting	Fish (unidentified species)	**Tool-assisted fish catching** A large male brown capuchin used small pieces of tomato, potato, or banana as bait to lure and catch fish; three individuals were also observed unsuccessfully using a bait, albeit two of them often accompanied and watched the large male.	Mendes et al. (2000)
	Bearded capuchins (*Sapajus libidinosus*)	Serra das Almas (Brazil)	Forest	Rocky cavy (*Kerodon rupestris*)	**Social hunting/meat sharing** A group of five bearded capuchins chased and trapped a rock cavy in a crevice; the largest male subsequently killed the rock cavy and then ate and shared the carcass with other males; given the lack of communication or division of roles between hunters, the authors report no signals of coordination or collaboration in the predation event.	Filho et al. (2021)
	Robust capuchin monkeys (*Sapajus* sp.)	Foz do Iguaçu (Brazil)	Forest	Domestic chicken (*Gallus domesticus*)	**Meat sharing** An adult male preyed upon a domestic chicken and then shared the carcass passively with two juvenile individuals.	Bender and Aguiar (2025)
	Brown/tufted capuchins (*Sapajus apella*) (formerly *Cebus apella*)	Tietê Ecological Park (Brazil)	Artificial setting	Bird (unidentified species)	**Meat sharing** Diverse sequences of food transfer (from scrounging to passive meat-sharing) were reported among a semi-free group of brown capuchins; meat sharing occurred principally between males or males to females.	Ferreira et al. (2002)
				Rat (*Rattus rattus*)	**Meat sharing** A dominant male brown capuchin ate an adult male rat (though the hunting episode was not observed) and shared the carcass with an immature monkey; a female juvenile then ate parts of the carcass, which fell on the ground.	Resende et al. (2003)
Cebus	White-faced capuchins (*Cebus capucinus*)	San Martín (Colombia)	Gallery forest	Brumback's night monkey (*Aotus brumbacki*)	**Passive scavenging?** A group of capuchins fed on a dead female brumback's night monkey apparently found in a tree hole by a male (no visible or audible evidence of hunting activity was reported by the authors).	Carretero-Pinzón et al. (2008)
		Lomas Barbudal (Costa Rica)	Forest	White-nosed coati (*Nasua narica*)	**Meat sharing** Incidents of meat transfer primarily involved adult females sharing with their less-than-1-year-old offspring.	Perry and Rose (1994)
		Santa Rosa (Costa Rica)	Forest	Variegated squirrel (*Sciurus variegatoides*) Several bird species	**Meat sharing** Most occurrences of meat transfer involved tolerated scrounging or co-feeding; active sharing was rare, being	Rose (1997)

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Table 3 (*continued*)

Genus	Species	Site	Ecosystem	Prey type	Cognitive skill(s)/behaviour pattern(s)	Source(s)
					observed only on four occasions between nulliparous females and infants and between males and infants.	

(Watts, 2020), it can nonetheless be postulated that the level of sensible qualities involved in meat-eating behaviour may have played a crucial role in modulating its continuity and intensity. In other words, the high degree of bodily exposure to organic matter (e.g., pathogenic agents, body fluids/tissues, and stick tools) within trophic dynamics could have paved the way for the evolution of more complex forms of relationships with prey taxa. The evolutionary consequences of this behaviour are hence to be assessed by cross-species comparisons.

4. Forms of embodied cognition and modes of vertebrate predation by extant primates

4.1. Elements of tool-assisted vertebrate predation

Tool usage in extractive foraging activities has been reported in some species (mainly birds and mammals) of the animal kingdom. For example, New Caledonian crows (*Corvus moneduloides*) predate on invertebrates by inserting plant material (modified twigs and *Pandanus* spp. leaves) into tree holes (Hunt, 1996); burrowing owls (*Athene cunicularia*) use mammalian dung to attract dung beetles (*Phanaeus igneus*) their principal prey (Levey et al., 2004); Goffin's cockatoos (*Cacatua goffiniana*) manufacture and employ up to three different kinds of wooden tools to extract seed matter of *Cerbera manghas* (O'Hara et al., 2021); sea otters (*Enhydra lutris*) open molluscs by pounding them against a stone balanced on the chest (Hall and Schaller, 1964); North American badgers (*Taxidea taxus*) prey on Richardson's ground squirrels (*Urocitellus richardsonii*) by moving wood blocks towards tunnel openings to entrap the prey (Michener, 2004); and bottlenose dolphins (*Tursiops* sp.) carry sponges (*Echinodictyum mesenterinum*) on their rostra as likely foraging tools (Smolker et al., 1997). Interestingly, among mammals, primates stand out as the most skilled tool users within the animal kingdom, a cognitive achievement perhaps only comparable to the Corvidae (Seed and Byrne, 2010). The stone-tool-aided extractive foraging episodes reported among long-tailed macaques (*Macaca fascicularis*: Luncz et al., 2017; Proffitt et al., 2018), capuchin monkeys (*Sapajus* and *Cebus* spp.: Ottoni and Izar, 2008; Luncz et al., 2016; Barrett et al., 2018), and Western chimpanzees (*Pan troglodytes verus*: Boesch and Boesch, 1983; Ohashi, 2015) indeed indicate advanced forms of sensorimotor intelligence.

It is important to note, however, that tool-assisted vertebrate predation is rare among extant metazoans, being only reported in a few taxa: the moving of wood blocks to plug openings into burrow systems to capture ground squirrels by North American badgers (*Taxidea taxus*: Michener, 2004) and the use of sticks as bird lures (*Egretta* spp.) by crocodilians (*Crocodylus palustris* and *Alligator mississippiensis*: Dinets et al., 2015) are likely to be extraordinary behavioural incidents. Similarly, as shown by Tables 2 and 3, tool usage in vertebrate predation appears limited to a few reports illustrating a high behavioural variation within and between primate species. For example, in Fongoli, Senegal (Pruetz and Bertolani, 2007); Mahale, Tanzania (Huffman and Kalunde, 1993; Nakamura and Itoh, 2008); and Moukalaba, Gabon (Wilfried and Yamagiwa, 2014), chimpanzees exhibit high levels of cognitive engagement with plant materials that provide the necessary conditions for the manufacture of tools; consequently, the degree of modification, use, and relation with plant matter not only determine the potential acquisition of prey but may also create opportunities for social learning and transmission. The same patterns might be inferred from the potential cases of tool-assisted hunting reported in Ndoki, Republic of Congo, and Batan, Senegal (Kuroda et al., 1996; Micheletti et al., 2022). Further, the Taï (Côte d'Ivoire) and Rekambo (Gabon) behavioural occurrences are also illuminating, given the nature of the chimpanzee-plant relationships involved in meat-eating dynamics. In Taï, for example, chimpanzees extract bone marrow with sticks and crack open monkeys' skulls by banging them against tree trunks (Boesch and Boesch, 1989); in Rekambo, on the other hand, chimpanzees smash the plastrons of hinge-back tortoises (*Kinixys erosa*) against a trunk and likely store meat in a tree (Pika et al., 2019). These sequences of chimpanzee-plant interconnectedness, therefore, show the highly relational qualities of chimpanzee meat-eating strategies, whether in the form of incipient percussive technology (tree trunks as proto tools for smashing vertebrate hard tissues), sophisticated tool-aided extractive behaviour (the modification of sticks for bone marrow extraction) or the more cognitively demanding food storage behaviour (a tree fork as a potential meat container).

Moreover, it is noteworthy that the chimpanzee's sister taxon, the bonobo (*Pan paniscus*), primarily exhibits tool-using behaviour in non-foraging contexts (Samuni et al., 2022), likely lacking the intrinsic motivation to manipulate objects (Koops et al., 2015) essential to patterning modes of tool-assisted meat consumption. However, other phylogenetically distant species may have acquired parallel concepts of folk physics by successfully acting upon the world (Kacelnik, 2009) in ways that converge with chimpanzee tool-use behaviour. The bodily and cognitive engagement with raw materials (e.g., plants) shown by the patterns of predation of Bornean orangutans (*Pongo pygmaeus*: Russon et al., 2014) and bearded capuchins (*Sapajus libidinosus*: Falótico and Ottoni, 2014; Falótico, 2023) may well illustrate cultural traditions bolstered by ramified behavioural proclivities which, in turn, emerge from elementary cognitive modules. Alternatively, convergent evolution could also be taken as a plausible explanatory framework for how particular modes of meat procurement (spear-like tools to hunt or fish) occur in these taxa. On a more theoretical level, the plant-tool use behaviour (jabbing with sticks to acquire prey) of *Pan troglodytes, Pongo pygmaeus,* and *Sapajus libidinosus* likely show ancient cognitive traits activated accidently in each socio-ecological setting. On a more empirical level, species' behavioural plasticity may have acted upon local environmental conditions, devising novel forms of tool-assisted meat acquisition strategies.

Nevertheless, at both ends of the spectrum (one based on speculative reasoning and another on localised empirical realities), we have, as a point of conjunction, the compenetration of agential qualities that may initiate under certain socio-material circumstances potentially innovative foraging behaviours (Bandini and Harrison, 2020) embedded in varied evolutionary pathways. In this light, the divergent behavioural predispositions in chimpanzee and bonobo tool use, likely caused by the Pleistocene environmental conditions (Furuichi et al., 2015), might hence be viewed as a phenomenon whereby a composition of cognitive traits has been allocated and/or activated patchily between these sister taxa. Experimental evidence, for instance, indicates that captive and semi-captive bonobos exhibit tool-assisted extractive foraging capabilities, thus corroborating the postulate of shared traits with chimpanzees (Roffman et al., 2015); nevertheless, those sensorimotor attributes are likely to be contingent on specific socio-environmental influences (Haslam, 2013) and, therefore, a kind of behavioural unpredictability is expected in the potential tool-aided technology of the primate lineage.

In summary, if chimpanzees (*Pan troglodytes*), bearded capuchins (*Sapajus libidinosus*), and Bornean orangutans (*Pongo pygmaeus*) exhibit an analogous pattern of tool-assisted foraging (be it for hunting bush-babies, *Galago senegalensis*: Pruetz and Bertolani, 2007; Pruetz et al.,

2015; squirrels, *Protoxerus stangeri/Heliosciurus rufobrachium*: Huffman and Kalunde, 1993; Nakamura and Itoh, 2008; mongooses: Wilfried and Yamagiwa, 2014; lizards, *Tropidurus* ssp.: Falótico and Ottoni, 2014; Falótico, 2023; or attempting to catch walking fish: Russon et al., 2014), high level of relations with plant matter should be at stake. This, of course, is well documented by these species' bodily engagement with plant tools (i.e., the degree of modification and/or manipulation of raw materials from the vegetal world) that enable them to penetrate particular trophic niches and then expand their dietary breadth (hence augmenting the species' nutritional intake) even amongst a primate of low-level carnivorous behaviour such as the orangutan.

Thus, the malleability of plant matter, alongside the high degree of primates' sensorimotor and phenomenal qualities involved in tool shaping and usage (from rousing to jabbing the prey), likely hints at the deep evolutionary roots of primate plant tool-use behaviour. It is thus highly likely that the LCA of panins or even of *Homo* and *Pan* used plant tools for foraging activities (Haslam, 2014). Yet, as shown by the use of food (fruits and vegetables) to lure and catch fish by brown capuchins (*Sapajus apella*) and the manipulation of stick tools by Bornean orangutans (*Pongo pygmaeus*) and bearded capuchins (*Sapajus libidinosus*) to catch fish and hunt reptiles and mammals respectively (Mendes et al., 2000; Falótico and Ottoni, 2014; Russon et al., 2014; Falótico, 2023), it is reasonable to believe that, throughout its evolutionary history, the primate predatory pattern might have depended significantly on the use of plant tools.

As with chimpanzee termite fishing, which, from a cognitive point of view, shows a wide array of behavioural and cultural variants in the modalities of plant-tool selection and alteration (i.e., variation in plant parts/materials modified and used as tools: bark, herb, stick) (Suzuki et al., 1995; Sanz et al., 2004, 2009; Almeida-Warren et al., 2017; Pascual-Garrido and Almeida-Warren, 2021); interestingly, the plant tool-using behaviour exhibited by the aforementioned primates in vertebrate predation shows, albeit in less degree of complexity, similar relational patterns of behaviour. The intensity of primate-plant interactions may well be the primary trigger of haptic experiences, e.g., 92% of tool source species (raw materials to manufacture termite-fishing tools) are also exploited for food by the Issa chimpanzees of Western Tanzania (Almeida-Warren et al., 2017). Perceptual experiences, however, are likely to be augmented by the immersive nature of tool-assisted meat acquisition and consumption; that is, phenomenologically speaking, the compenetration of organic matter (vegetal and animal) may stimulate higher-order levels of perception and instil novel forms of interspecies relationalities. That said, the mounting evidence of primate plant tool use, ranging from rudimentary digging tools for underground storage organs (USOs) extraction (Hernandez-Aguilar et al., 2007) to the more complex wooden spears for vertebrate hunting (Pruetz and Bertolani, 2007; Falótico, 2023), might shed light on the "archaeologically invisible" perishable tools (Almeida-Warren et al., 2017; Pascual-Garrido and Almeida-Warren, 2021; Pascual-Garrido et al., 2025) likely used by the earliest hominins. Plant tool use in vertebrate predation and carcass processing is therefore likely an ancient behaviour pattern (Pruetz and Bertolani, 2007; Russon et al., 2014; Milks et al., 2026); its evolutionary significance is nevertheless to be assessed by solid empirical observations and theoretical models.

4.2. Prosocial behaviour: meat sharing and cooperative hunting

Based on Tables 2 and 3, most instances of meat sharing exhibited by primates appear to be primarily passive and involve a certain degree of social tolerance (e.g., *Nomascus concolor jingdongensis*, *Pongo abelii*, *Papio* spp., and *Cebus* spp., but see O'Hearn et al., 2025 for an analysis of complex passive meat sharing patterns and tolerant behaviour among the multi-level society of Guinea baboons of the Niokolo Koba National Park, Senegal); however, the only exceptions to this behavioural tendency are *Pan* spp., which occasionally show active forms of meat sharing. For example, in the forests of Taï, Côte d'Ivoire (Boesch and Boesch, 1989) and Rekambo, Gabon (Pika et al., 2019), chimpanzees have been observed actively and cooperatively sharing the meat of red colobus monkeys (*Piliocolobus badius*) and hinge-back tortoises (*Kinixys erosa*), respectively. On the other hand, in the forests of LuiKotale and Kokolopori, Democratic Republic of the Congo, bonobos exhibit patterns of out-group social tolerance and therefore meat seems to be actively and peacefully shared between bonobo groups (Fruth and Hohmann, 2018; Samuni et al., 2020). Interestingly, this pattern of behaviour clearly illustrates that, unlike the highly hostile relations exhibited by chimpanzees towards outsiders, bonobos display high levels of intergroup interactions, such as the reciprocal exchange of food (Samuni and Surbeck, 2023).

Regarding cooperative hunting, Strum (1975) reported rudimentary forms of this behaviour among savanna olive baboons (*Papio anubis*) in Gilgil, Kenya. In the forest of Serra das Almas, Brazil, bearded capuchins (*Sapajus libidinous*) have been observed hunting a rocky cavy (*Kerodon rupestris*) socially; however, Filho et al. (2021) reported that no forms of cooperation had been involved in this instance. Besides the elementary forms of cooperative and social hunting exhibited by olive baboons and bearded capuchins, respectively, chimpanzees are the only primate species showing complex patterns of cooperative hunting behaviour. In the Taï forest, for instance, Boesch and Boesch (1989) and Samuni et al. (2018) reported that chimpanzees exhibited high levels of cooperative hunting; hence, according to Samuni et al. (2018), the number of hunters who cooperate is likely to be directly proportional to the hunting success and meat sharing. It is also worth mentioning the potential act of cooperative tool-assisted hunting documented by Wilfried and Yamagiwa (2014) amongst the chimpanzees of the forest of Moukalaba, Gabon. This fascinating occurrence involved a dyad of male chimpanzees utilising two sticks of *Afrostyrax lepidophyllus,* likely as tools to chase and rouse a prey (probably a mongoose) hidden in a log.

The abovementioned forms of prosocial behaviour (cooperative hunting and meat sharing) exhibited by some primates may have important implications for the evolution of meat-eating strategies within the hominin lineage. This may also point to the ramifications, variations, and commonalities of cognitive and/or behavioural traits, as demonstrated, for example, by the meat-sharing patterns of our closest biological relatives, chimpanzees and bonobos, as well as those exhibited by Guinea baboons (*Papio*: O'Hearn et al., 2025); these behavioural repertoires likely hint at a shared underlying structure operating also within forms of intra/intergroup and multi-level meat transmission patterns exhibited by hunter-gatherer and hunter-horticultural societies (Sharanahua: Siskind, 1973; Ju/'hoansi: Wiessner, 2002; Tsimane': Gurven and von Rueden, 2006; Mayangna/Miskito: Koster, 2011; Hadza: Wood and Marlowe, 2013; Agta/Mbendjele: Dyble et al., 2016; Shuar: Abad Espinoza, 2025; Abad Espinoza & Fleck, Forthcoming). It could therefore be argued that rudimentary (e.g., kinds of social and cooperative hunting shown by *Sapajus libidinous* and *Papio anubis*) and more complex (e.g., multi-level and between-group meat sharing patterns in *Papio* and *Pan paniscus*, respectively and cooperative tool-assisted vertebrate predation in *Pan troglodytes troglodytes*) forms of prosociality exhibited by the predatory behaviour of these primate species denote behavioural patterns likely present (though probably in a combined form) among the earliest hominins. These forms of prosociality, moreover, are deeply grounded in complex interspecies entanglements and forms of embodied interactions and sensory engagement with animal matter that have further increased over the course of hominin evolution.

4.3. Elemental scavenging patterns

Data from Tables 2 and 3 suggest that scavenging is rare and most inferred and/or observed behavioural incidents are primarily reported in its passive form among snub-nosed monkeys (*Rhinopithecus bieti*: Ren et al., 2010), Bornean orangutans (*Pongo pygmaeus*: Buckley et al.,

2015), Sumatran orangutans (*Pongo abelii*: Sugardjito and Nurhuda, 1981), tufted capuchins (*Sapajus apella*: Carretero-Pinzón et al., 2008), yellow baboons (*Papio cynocephalus*: Hausfater, 1976), grey-footed chacma baboons (*Papio ursinus griseipes*: Allan et al., 2022) and chimpanzees (*Pan troglodytes schweinfurthii*: Hasegawa et al., 1983; Muller et al., 1995; Hosaka et al., 2001; Watts, 2008). Setting aside the indirect evidence (i.e., a faecal sample containing the body parts of a black-crested Mangabey, *Lophocebus aterrimus*) of a potential incident of kleptoparasitic behaviour (meat-stealing from predators, e.g., *Stepahnoaetus coronatus, Felis aurata, Panthera pardus*) reported by Surbeck et al. (2009) among LuiKotale bonobos, confrontational scavenging thus appears restricted to chimpanzees and *Papio* spp.

For example, in Tanzania, among the Gombe chimpanzees (*Pan troglodytes schweinfurthii*), Morris and Goodall (1977) documented several instances of carcass thefts (bushbuck [*Tragelaphus scriptus*] and helmeted Guinea fowl [*Numida meleagris*]) from olive baboons (*Papio anubis*). Likewise, in the Mahale Mountains, Hosaka and Ihobe (2015) reported that chimpanzees stole a blue duiker (*Philantomba monticola*) carcass from a small ambush predator (probably an African civet [*Civettictis civetta*] or ratel [*Mellivora capensis*]). Hasegawa et al. (1983) and Hosaka (2015) also reported two potential cases of power scavenging in which chimpanzees likely appropriated a bushbuck (*Tragelaphus scriptus*) and a red colobus (*Procolobus tephrosceles*) carcass from a leopard (*Panthera pardus*), respectively. Yet Nakamura et al. (2019) recently reported the only documented occurrence of power scavenging among chimpanzees; thus, a group of Mahale chimpanzees seems to have deprived a leopard (*Panthera pardus*) of a freshly killed blue duiker (*Philantomba monticola*). Worthy of note is also a recent incident of confrontational scavenging documented by Baker et al. (2024) in the Issa Valley, in which chimpanzees stole a bushbuck (*Tragelaphus scriptus*) carcass from a crowned eagle (*Stephanoaetus coronatu*).

Among *Papio* spp., on the other hand, three cases of confrontational scavenging have been documented so far. In the Mashatu Game Reserve, Botswana, Branch (2017) has observed grey-footed chacma baboons *Papio ursinus griseipes*) stealing a helmeted Guinea Fowl (*Numida meleagris*) carcass from a Tawny Eagle (*Aquila rapax*). In the Tswalu Kalahari reserve and Hluhluwe-iMfolozi park (South Africa), Davis et al. (2024) have recently reported two occurrences of kleptoparasitic behaviour (in the form of power scavenging) in which chacma baboons (*Papio ursinus*) deprived a cheetah (*Acinonyx jubatus*) of a springbok (*Antidorcas marsupialis*) and an impala (*Aepyceros melampus*) carcass, respectively. Additionally, two instances of baboons confronting cheetahs for the potential acquisition of vertebrate matter (in fact, these were not included in our dataset since no meat consumption by baboons was recorded in both cases and therefore did not represent a proper scavenging behaviour) have been reported by Davis et al. (2024). The first involved chacma baboons of the Kruger National park (South Africa), chasing away a cheetah from an impala carcass, and the second olive baboons (*Papio anubis*) of the Maasai Mara (Kenya), depriving a cheetah of a Thomson's gazelle, *Eudorcas thomsonii* (albeit the prey was still alive before being killed by a baboon).

The aforementioned proven and potential instances of confrontational scavenging behaviour exhibited by chimpanzees and baboons may thus represent evolutionary precursors of hominin meat consumption patterns (Dominguez-Rodrigo and Pickering, 2017; Willems and van Schaik, 2017; King, 2024). By actively confronting hypercarnivores like birds of prey (*Stephanoaetus coronatu* and *Aquila rapax*) and felids (*Panthera pardus* and *Acinonyx jubatus*), these primate taxa are capable of depriving dangerous predators (as in the case of leopards and cheetahs) of important animal resources. Evolutionarily speaking, defensive and/or counter-attack mechanisms are likely the primary triggers of the confrontational scavenging patterns (Willems and van Schaik, 2017; Davis et al., 2024) exhibited by these primate species; these may hence have played a key role in the further evolution of the cooperative meat-eating strategies (confrontational scavenging and cooperative hunting) exhibited by early *Homo* (Willems and van Schaik, 2017).

Although carrion avoidance in extant primates (and probably early hominins) likely operates as a protective mechanism against pathogenic contamination (Ragir et al., 2000; Smith et al., 2015), our dataset indicates that confrontational scavenging opportunities involved primarily freshly killed carcasses; consequently, it is expected that apart from strategies of carrion selection, cooking and marrow extraction (as forms of reducing pathogen load), early hominins may have consumed within a few hours freshly killed carcasses, thus avoiding bacterial contamination (Smith et al., 2015). Amongst primates, however, humans are the only species whose stomachs have an extremely low pH of gastric acid (pH = 1.5), similar to those of carrion eaters; scavenging behaviour may therefore have played a pivotal role in the evolution of stomach acidity in humans (Beasley et al., 2015; Fujimori, 2020; Mateos et al., 2025) to cope with the high levels of pathogenic parasites and bacteria associated with carrion (Ben-Dor et al., 2021). This aligns strongly with the ethnohistoric and ethnographic records that show patterns of putrefied meat and fat consumption (and hence organic matter infested with maggots [Diptera larvae]) among tropical and circumpolar peoples, hinting at ancient forms of feeding behaviour likely exhibited by Palaeolithic hominins (Speth, 2017, 2019, 2024, 2025; Speth and Morin, 2022). Notably, this pattern is further corroborated by a recent study led by Beasley et al. (2025), which suggests that the high $\delta^{15}N$ values observed in Neanderthals were likely caused by the frequent consumption of maggots associated with rotten animal matter.

Alternatively, by intensifying the plant-based self-medication strategies found in primates, ancient humans could have dealt with the increased pathogen load within an increasingly carnivorous dietary niche (Hagen et al., 2023). Both biological (i.e., stomach acidity and gut microbiota) and behavioural (i.e., plant-based self-medication strategies) characteristics of humans (and probably early hominins) seem to have been fundamental for their energy-rich diet, based (albeit in part) on scavenged meat; this therefore would have allowed archaic hominins to handle the wide variety of parasites and bacteria (from Taeniid tapeworms: Hoberg et al., 2001 to *Helicobacter pylori:* Tourrette et al., 2024) associated primarily with raw and/or rotten animal tissues. In sum, scavenging behaviour—besides being a viable mode of acquiring energy-rich animal-based resources—appears to have been a strong centripetal force throughout hominin evolution, exemplified by high levels of bodily immersion in intimate interactions between physicalities that have further triggered a wide array of organismic encounters, multisensory experiences, and interspecies possibilities.

5. Implications of primate carnivory for the evolution of human relational ecologies, socio-cognitive and onto-epistemological frameworks

It has been suggested that certain behavioural traits (e.g., cooperative hunting of large game, food sharing, group defence) exhibited by social carnivores like spotted hyenas (*Crocuta crocuta*) and wolves (*Canis* spp.) are likely to be more convincing referential models for understanding hominin carnivory than those of non-human primates (Schaller and Lowther, 1969; Thompson, 1975; Smith et al., 2012; Cosans, 2023). It might then be inferred that, apart from patterns of tool-assisted predation exhibited by some primates, the social carnivores virtually excel in all forms of cooperative (hunting/scavenging of large mammals) meat-eating behaviour; thus, it is conceivable that primary forms of faunivory shown by hominins are to be found within the carnivores (Thompson, 1975). Leaving aside significant elements of convergence between archaic hominins and extant carnivores (Smith et al., 2012), the most basic forms of meat-eating behaviour likely exhibited by our hominin ancestors are present (although patchily distributed) in phylogenetically and anatomically close species.

As noted above, the carnivorous behaviour of extant non-human primates evinces important patterns of meat consumption (i.e., scavenging, tool use, cooperative hunting, meat sharing) of paramount

importance to delineate the potential evolutionary pathways of human carnivory. These elementary structures of faunivory may thus help reconstruct hypothetical forms of subsistence strategies that, cognitively and behaviorally speaking, have gradually amplified in the hominin clade. Based on our dataset and theoretical framework, a likely evolutionary scenario might be suggested for the emergence and further intensification of carnivory in the hominoid lineage. At a more granular level, this may unveil how the evolution of primate carnivorous feeding behaviour was inextricably intertwined with forms of interspecies intimacy, bodily interactions, and sensory engagement; from this compenetration of physicalities and the further increase of intensity of associated relational processes, a suite of phenomenal qualities and world-making processes may have gradually emerged in our genus.

1. The last common ancestor of *Pan* and *Homo*, as well as other archaic hominoid species, may have exhibited a combination of meat-acquisition patterns (although present in different degrees and intensities in those species and aimed mainly at the consumption of small prey), primarily involving opportunistic/ambush predation, plant-tool-assisted technology, and passive/confrontational scavenging. At this stage, the degree of contact intensity with animal matter and the associated embodied and interspecies interactions may have been similar to those exhibited by some living non-human primates.
2. Prosocial behaviours such as cooperative hunting/scavenging and meat sharing may have begun to appear; however, these traits might not have achieved levels beyond a chimpanzee-bonobo model, likely due to ecological (i.e., constraints on prey size) and socio-cognitive factors. Forms of bodily immersion in the predatory niche and related interspecies intimacy and cognitive engagement may have paralleled (at least partly) those of the first stage.
3. More complex forms of cognition and social behaviour may have emerged during the Plio–Pleistocene, when early hominins began to acquire large animals via passive/confrontational scavenging, hence enabling them to exploit a vast amount of animal matter, including within-bone resources, through the aid of organic and inorganic materials used as tools. This dietary expansion allowed hominins to assimilate significant nutritional elements in the form of protein, fat and micronutrients; selection may thus have favoured increased cognitive capabilities critical for the new trophic level occupied by hominins, typified by higher levels of bodily and cognitive–sensory engagement with animals and novel forms of multispecies associations.
4. A complete immersion into the carnivore guild by means of scavenging and hunting of large mammalian prey reached its zenith; this, therefore, likely involved profound embodied associations between hominins and a wide variety of organismic kingdoms (from animal predators/scavengers to parasites to bacteria to plants), lithic materials, water sources, and the further use of fire. Built upon these highly complex forms of interspecies intimacy and compenatration of matter and agential qualities, this stage would have opened the way for the evolution of hominin technical behaviour (i.e., tool-making, cooking, self-medication strategies) and the emergence of abstract thinking.
5. Primary forms of ritual behaviour (i.e., rock art, special treatment of animal remains, food taboos, shamanic practices) towards large animals, coupled with elements of mytho-cosmological and ontological understanding, began to appear in the behavioural and cognitive repertoire of Palaeolithic hominins. The continuity and maximum manifestation of these traits (with the exception of rock art) are exhibited by extant hunter-gatherers and were likely heavily dependent on elevated and continuous exposures to embodied and cognitive-sensory interactions with animals and other entities from the biological and inorganic world; forms of social and emotional bonding towards animals, as well as specific phenomenal experiences and subjective qualities derived from animal-human relationalities may thus have served as the scaffold for the construction of life-worlds and activation higher-order relational processes.

5.1. *Pre-lithic hominid carnivory*

Let's elaborate on the intricacies of the hypothetical evolutionary trajectories of hominin faunivory illustrated above. On the basis of an ancestral prototype of ambush predation and patterns of insectivory (Wu et al., 2022), the earliest hominids—species perhaps stretching back millions of years before the *Pan-Homo* split—likely exhibited an amalgamation of behavioural traits, ranging from tool-aided hunting behaviour to scavenging (whether in its passive or confrontational forms) of small animals. In this first stage, therefore, the last common ancestor of chimpanzees and humans (Dominguez-Rodrigo and Pickering, 2017; Wood and Gilby, 2017) may have hunted small prey; interestingly, as argued by Bertacchi and Watts (2023), the faunal assemblages (mainly small animals such as colobines and Testudines) associated with hominoid species (e.g., *Orrorin tugenensis*: Pickford and Senut, 2001; Senut et al., 2001; *Sahelanthropus tschadensis*: Vignaud et al., 2002; *Ardipithecus ramidus*: WoldeGabriel et al., 1994; White et al., 2009) likely provide interesting clues to detect the carnivorous behaviour of pre-lithic hominins (Bertacchi and Watts, 2023). Further, this pattern of predation was likely displayed alongside plant-tool-assisted technology (possibly stick tools used for rousing and jabbing the prey, as found among chimpanzees and capuchin monkeys) (Marlowe, 2005; Pickering and Dominguez-Rodrigo, 2010) and passive and/or power scavenging behaviour, as exhibited primarily by chimpanzees and baboons.

The second stage may have developed coevally with the first stage, as more sophisticated forms of prosocial behaviour may have begun to appear in our primate ancestors. Specifically, behavioural characteristics such as active meat-sharing in combination with cooperative hunting and/or scavenging could have been exhibited by any hominoid, albeit variations in the patterns of behaviour (and hence a diverse emphasis on behavioural traits) among those species were likely; a predatory behaviour focused primarily on small animals plus complex forms of prosociality (as documented by chimpanzee and bonobo patterns of cooperative hunting and meat sharing, respectively) may have been an evolutionary scenario that likely lasted for a time period between 13 and 4 Ma until the appearance of the australopithecines. Although the earliest hominids may have exhibited embodied associations with animal matter (insects and vertebrates) and forms of interspecies intimacy similar to those found among modern primates, subsequent stages of animal-hominin relationships may have nevertheless built on pre-existing embodied forms of organismal interactions and lower-order relational processes.

5.2. *Emergent collisions of materialities: scavenging, stone tools, and the earliest embodied engagement with large animal carcasses*

The third stage may have emerged in the late Pliocene and is primarily associated with the onset of sporadic large-animal resource exploitation by hominins; this, therefore, likely activated novel forms of embodied associations with abundant animal matter and a wide variety of relational processes involving biological and inorganic agents. A recent study based on nitrogen isotope analysis of tooth enamel suggests, however, that *Australopithecus africanus* at Sterkfontein, South Africa (~3.5 Ma), had a primarily plant-based diet (Lüdecke et al., 2025). Although it is justifiable to believe on the basis of empirical evidence that meat-eating was minimal among *Australopithecus* (and hence similar to that observed among *Pan, Papio, Sapajus* and *Cebus* species), contemporaneous australopithecines living in other regions of Africa could have exhibited more regular meat-consumption patterns (Lüdecke et al., 2025); and, thereby, particular forms of embodied interactions

with animals and emergent forms of interspecies intimacy were highly likely during this time period. With that in mind, the earliest archaeological evidence of hominin carnivorous behaviour has been reported, for example, in Ethiopia at the localities of Dikika ~3.4 Ma (McPherron et al., 2010); Gona ~2.6 Ma (Domínguez-Rodrigo et al., 2005); Bouri ~2.5 Ma (Heinzelin et al., 1999); in Kenya at the locality of Nyayanga ~3 Ma (Plummer et al., 2023); in Algeria at the site of Ain Boucherit ~2.4 Ma (Sahnouni et al., 2018); and in the Masol Formation of the Siwalik Frontal Range of India ~2.6 Ma (Malassé et al., 2016). These localities provide strong indications that hominins (i.e., *Australopithecus afarensis* at Dikika, *Australopithecus garhi* at Bouri, *Paranthropus* sp. at Nyayanga) exploited large mammal carcasses (e.g., hippopotamids, bovids) through the aid of cutting and percussive stone tool technology, thus hinting at complex adaptive behaviours and specific modes of modification and bodily and sensory interactions with materialities likely unknown by earlier hominoid species.

But how did those hominins obtain large animal carcasses? Excluding the assumption that australopithecines hunted large prey—as one might expect for Pliocene hominins, who probably did not possess suitable weaponry—, passive and even confrontational scavenging may have been the most viable subsistence strategies for acquiring large prey. As Plio-Pleistocene African ecosystems began to exhibit variable climatic conditions, a decrease in woodland foods and an increase in megaherbivores (Plummer, 2004), the encounter of large mammal carcasses would likely have represented a great opportunity for hominins to expand their dietary niche. Nevertheless, scavenging on those carcasses was likely a risky undertaking, even if hominins exhibited primarily passive scavenging behaviour (Rodríguez et al., 2023); the likelihood of encounter with terrestrial predators and scavengers may have been high given the large amount of animal matter in the form of meat and bone marrow. The scavenging niche of hominin paleoecology is highly likely to have functioned as a strong centripetal force, attracting heightened forms of interspecies intimacies; this must thus have been a locus characterised by high levels of bodily exposure to intimate organismic interactions and agential powers.

Noteworthy in this regard is a new crocodile (*Crocodylus lucivenator*) from the Pliocene Hadar Formation of north-eastern Ethiopia (Brochu et al., 2026). Being the largest predator known from the Hadar Formation, this crocodylian species may have lived in close association with *Australopithecus afarensis,* whose life depended on water (Brochu et al., 2026). From these hominin-environment relationalities, I can infer that, since *Australopithecus afarensis* must have regularly visited water sources for hydration, intimate encounters with *Crocodylus lucivenator,* dead animals, and other predators/scavengers are likely to have been extremely high. Therefore, feeding on carrion near water sources must have triggered a wide array of intimate interspecies encounters (e.g., hominin-crocodile) and embodied interactions highly dangerous for our ancestors. In accordance with this trophic scenario, recent research suggests that, like australopithecines, *Homo habilis* may have been preyed upon by leopards (although a smaller and less dangerous predator than *Crocodylus lucivenator*), thus indicating that the shifting in the balance of power with other carnivores did not occur among these hominin species (Vegara-Riquelme et al., 2025). However, based on the scavenging patterns of baboons (Davis et al., 2024) and chimpanzees (Nakamura et al., 2019), a group of hominins may well have driven off solitary carnivores, such as cheetahs and leopards, from a carcass. Ruxton and Wilkinson (2013) postulated, for instance, that a well-coordinated group of hominins armed with wooden thrusting spears might have been able to drive off lions and hyenas. Kortlandt (1980) also inferred from experimental evidence that early hominins likely used thorny branches as both a defence mechanism and to rob carnivores of their freshly-killed meat. Treves and Naughton-Treves (1999) reported that contemporary humans in rural Uganda, armed with spears, drove carnivores from kills; thus, deducing that, if acting in a cooperative and coordinated fashion, early hominins may have been able to drive carnivores from kills using stone tools or long sticks.

It seems therefore plausible that, at least in theory, group cooperation (at least minimally), the use of rudimentary technology (thorny branches, sticks, spears, stone tools and thus the capacity of aimed throwing) and loud vocalisations (e.g., waa barks emitted by chimpanzees to intimidate predators) would have been behavioural characteristics likely exhibited by hominins critical for scavenging large mammal carcasses (Bickerton and Szathmáry, 2011; Nakamura et al., 2019; Mateos et al., 2025). Furthermore, environmental clues such as circling vultures (Ruxton and Wilkinson, 2013) or the calls of mammalian carnivores likely aided hominins in locating carcasses, as documented among the Hadza of Tanzania (O'Connell et al., 1988). Combined, this suite of behavioural and cognitive traits would have further enhanced the scavenging opportunities among early hominins; immersion in the scavenging niche would have likewise been heavily dependent on heightened levels of embodied and sensory associations with actants from the biological and inorganic world.

But apart from scavenging large animals, the most prominent behaviour that set apart our Pliocene ancestors from our primate relatives was the use of implements for carcass processing. Amongst primates, the only rare instances of tool-assisted carcass processing have been documented in chimpanzees; these range from the extraction of brain tissue and bone marrow using a leaf wad[2] or sticks, respectively (Teleki, 1975; Boesch and Boesch, 1989) to percussive proto-tool use (i.e., banging skulls and plastrons against tree trunks) aimed at the acquisition of inside-bone nutrients (Boesch and Boesch, 1989; Pika et al., 2019). Yet these rudimentary forms of percussive technology involved in meat processing do not represent a rigorous replication of percussive behaviours aimed at the acquisition of plant matter (e.g., nut cracking) widely reported in chimpanzees, macaques, and capuchins (Boesch and Boesch, 1983; Ottoni and Izar, 2008; Ohashi, 2015; Luncz et al., 2016, 2017; Proffitt et al., 2018; Barrett et al., 2018). Quite remarkably, though chimpanzees do not transfer their nutcracking skills to marrow extraction by using tools to open bones (Bertacchi and Watts, 2023), experimental evidence suggests that chimpanzees and bonobos are cognitively equipped to learn how to crack bones using tools (Kitahara-Frisch et al., 1987; Roffman et al., 2015).

It is, therefore, reasonable to infer that although primate stone-tool-aided extractive foraging (e.g., nut cracking) likely represents a cognitive template from which similar percussive behaviours (marrow extraction) developed in Oldowan hominins (Eren et al., 2025), primary forms of percussive technology (chimpanzee-like percussive proto-tool use aimed at the acquisition of inside-bone nutrients) may have been behavioural patterns exhibited by pre-lithic hominins and precursors of more complex forms of percussion tools for carcass processing. This evolutionary scenario is thus consistent with the assumption that percussion scavenging may have been the most basic form of predation aimed primarily at exploiting fatty-rich foods such as bone marrow and brain tissues (Thompson et al., 2019). Interestingly, this behaviour may not have necessitated the use of stone tools (that is, a behaviour that predated the Oldowan and perhaps earlier technocomplexes like Lomekwi (~3.3 Ma); Harmand et al., 2015) in that perishable materials (e.g., tree trunks, roots, bones) may have functioned as percussive tools to access within-bone nutrients (Thompson et al., 2019; Eren et al., 2025). Eren et al. (2025) propose, for instance, that this percussion scavenging scenario (i.e., the smashing of bones for marrow extraction) triggered a sequence of behavioural processes epitomised by (1) the appearance of cutting behaviour (in the form of bone flakes produced during marrow acquisition used as tools to cut meat; see also Gürbüz and Lycett, 2021); (2) the use of natural, sharp-edged stone objects (naturaliths) as more effective cutting tools; and ultimately (3) the emergence of stone knapping as a by-product of the emulation of naturaliths. These sequential steps may, socio-cognitively speaking, be indicators of

[2] Due to the lack of information concerning the predation event, this was not included in our dataset.

cumulative cultural evolution since they appear to have depended on the gradual exploitation of natural phenomena (Derex, 2022), embodied by a wide range of materialities (flesh, bones, woods, stones) whose primary significance arose from percussion scavenging patterns (Eren et al., 2025) and intimate forms of hominin-matter interactions.

The exploitation of megaherbivore carcasses through percussion scavenging would have allowed Pliocene hominins to expand their trophic niche, thus prompting the initial immersion into the predator guild. For the first time in hominin evolutionary history, this novel trophic position exposed our ancestors to close associations with prey, predators, and scavenger animals. These primary forms of connections with animal taxa (Shipman, 2010) and, by extension, the early exposure to the predatory niche, laid the groundwork for a further set of bodily, biobehavioral and cognitive associations with physicalities; these are thus epitomised by the intimate relations hominins had with organic and inorganic materials used as tools, animal bodily fluids and tissues and zoonotic pathogens.

Tool-assisted meat processing patterns appear to have exerted strong evolutionary pressures on hominins. In this regard, Zink and Lieberman (2016) argue that tool use and meat-eating (and hence the dependency on extra-oral mechanical processing that facilitates the ingestion of meat) may have selected for the reduction of craniodental features. Besides the use of tools as meat tenderising techniques (slicing and pounding) (Zink and Lieberman, 2016; Ekström et al., 2025), the process of putrefaction and/or fermentation, could also have facilitated similar anatomical changes by softening and pre-digesting the meat of scavenged carcasses (Speth, 2017; Speth and Morin, 2022); however, this pattern of meat consumption is difficult to attest in the archaeological record (Ekström et al., 2025). The primary point is that early forms of stone-tool-aided extractive foraging and meat-eating behaviour (that is, a close interplay between the two) likely were catalysts of the evolution of a further set of biological, neurocognitive, behavioural and social elements (Aiello and Wheeler, 1995; Milton, 1999; Leonard et al., 2007; Stout et al., 2008; Navarrete et al., 2011; Hecht et al., 2015; Zink and Lieberman, 2016; Toth and Schick, 2018; Osiurak et al., 2021; Affinito et al., 2024). For example, the acquisition of a vast amount of energy-dense animal products, mainly due to the incorporation of percussive and cutting technology, may have opened the way to novel forms of sociality (Kennedy, 2005; Linares Matás and Yravedra, 2021). Nevertheless, it was the ingestion of fat (primarily in the form of inside-bone nutrients), a critical source of energy, and highly dependent on elementary forms of carnivory (percussive scavenging) and relational processes (i.e., high levels of bodily and cognitive engagements with biological agents and inorganic matter) that likely functioned as a primary trigger for the evolution of cognition (Osmo, 2024); consequently, the amplification of certain elements of prosocial and cognitive behaviour (from cooperation in carcass theft and defence to butchery and meat-sharing [see also Thompson et al., 2019]) likely signified a considerable enhancement of the preexisting *Pan*-like model of prosociality, thus paving the path for the further emergence of the genus *Homo*.

5.3. *Forms of embodiment and interspecies intimacy: Homo erectus, Neanderthals and the complexification of hominin-animal interactions*

Based on the major biological, behavioural and cognitive evolutionary changes undergone by hominins (particularly early *Homo*), the fourth stage is characterised primarily by heightened levels of embodiment associated with the complexification of hominin-animal entanglements and intricate forms of interspecies intimacy, spanning the Earlier Stone Age/Lower Palaeolithic and Middle Palaeolithic/Middle Stone Age. By about 2.0 and 1.7 Ma, for example, hominins from different localities in Africa and Eurasia exhibited complex patterns of acquisition and butchery of medium and large-sized carcasses (Bunn et al., 1986; Ferraro et al., 2013; Pante et al., 2018; Hanon et al., 2025; Dominguez-Rodrigo et al., 2026; Forrest et al., 2026). Notably, at Olduvai Gorge, Tanzania, hominins likely shared cooperatively large quantities of meat and marrow (Bunn et al., 1986). At the same locality, recent research suggests intense proboscidean butchery reflecting adaptive patterns of meat consumption and sharing of megafaunal resources among members of a large group (Dominguez-Rodrigo et al., 2026). Further, at Kanjera, Kenya, hominins also exhibited distinct scavenging strategies, primarily targeting fatty-rich within-head food resources, such as brain matter, mandibular nerve and marrow (Ferraro et al., 2013). New evidence from the Koobi Fora Formation in Kenya also shows that hominins exhibited persistent and flexible foraging behaviours—including early access to carcasses, selective transport of limbs, and systematic marrow extraction within riparian settings—, a consistent foraging niche maintained, as in other East African localities, across temporal and varied ecological contexts (Forrest et al., 2026). These forms of prosociality and foraging flexibility—epitomised by particular modes of consumption of animal matter (i.e., within-bone nutrients)—far exceed those found among extant non-human primates (Bunn et al., 1986); and again, it is logical to suppose that increased consumption of fat may have provided *Homo* the essential calorific base to further develop sophisticated forms of cognition (e.g., causal reasoning), thus fueling encephalisation (Osmo, 2024). At the most basic level, however, the assimilation of high-value animal products—whether in the form of bone marrow or fat-rich insects (Brömme et al., 2026)—and the consequent evolution of cognition are likely to have been highly determined by lower-order relational processes exemplified by a high degree of animal-hominin proximity and a wide variety of embodied interactions with physicalities and related perceptual experiences.

The use of cooking fire by *H. erectus* approximately 1.9 Ma may also have had important evolutionary and adaptive consequences (Wrangham and Carmody, 2010; Wrangham, 2017). These are indeed exemplified by the substantial increase in energy gained from meat (Carmody et al., 2011), the reduction in the cost of its digestion (Boback et al., 2007) and the neutralisation of dangerous pathogenic agents (Smith et al., 2015). As such, in combination with techniques that made meat easier to chew and digest (i.e., putrefaction/fermentation and the use of stone tools for pounding-slicing), the thermal processing of meat (albeit in sporadic natural fires) would thus have facilitated significant anatomical and cognitive changes (Ekström et al., 2025); interestingly, the acquisition of fermentation technology (and therefore the consumption of externally fermented foods, such as meat) by early hominins has recently been proposed as a primary metabolic trigger of hominin brain expansion (Bryant et al., 2023). Nonetheless, it is likely that the ingestion of fat from inside-bone nutrients (namely, a relatively safe food [see Smith et al., 2015]) and the subsequent increased consumption of meat, possibly due to cooking and the complexification of plant-based self-medication patterns (Hagen et al., 2023), may have accelerated the major biological and cognitive changes in our genus. Alternatively, as suggested by Ben-Dor and Barkai (2025), it was not cooking but the need to preserve and protect megaherbivore carcasses (and hence vast amounts of meat and fat) from predators and scavengers that acted as a main driver for early fire use in *H. erectus*. This hypothetical behavioural shift may therefore add a further level of understanding of the complex biosocial and cognitive evolution of the *Homo* species. And yet, the above-mentioned behavioural traits developed over the course of the evolution of *Homo* may point to intricate patterns of organismal entanglements and forms of hominin-environment relationalities saturated with agentiality and intimate corporeal encounters.

The gradual transition between non-*erectus Homo* (e.g., *H. habilis*) and *H. erectus*, likely due to the above-mentioned factors, has thus equipped the latter with sophisticated cognitive abilities and novel anatomical features (e.g., Wrangham, 2017). By ~ 1.2 Ma, in Eurasia, hominins may have exhibited complex cooperative scavenging behaviour to outcompete giant hyenas (*Pachycrocuta brevirostris*) for the acquisition of carrion (Rodríguez et al., 2023). During the same spatio-temporal frame, evidence suggests that a mammoth (*Mammuthus*

meridionalis) carcass found in a waterbody was scavenged by hominins and sabre-toothed cats (Yravedra et al., 2024). This therefore implies that, in order to face predators/scavengers and exploit megafauna effectively, hominins must have displayed high levels of sociality, communication, and sensorimotor skills (Mateos et al., 2025); both language and endurance running may have emerged from this trophic niche, fundamental traits that were likely part and parcel of the behavioural repertoire of *Homo erectus* (Bramble and Lieberman, 2004; Bickerton and Szathmáry, 2011), thus underscoring the critical role played by scavenging behaviour (Mateos et al., 2025) and its centripetal relational processes embedded in elevated interspecies intimacy and bodily and sensory interactions between actants throughout hominin evolution.

In this context, higher levels of physical and cognitive engagement with megaherbivores were achieved, as attested by the fashioning of hippopotamus and proboscidean bones into complex tools, documented in the African localities of Konso (1.4 Ma) and Olduvai Gorge (1.5 Ma) (Sano et al., 2020; de la Torre et al., 2025). This techno-behaviour aligns with other African and Eurasian Early Stone Age/Lower Palaeolithic sites, likely hinting at intimate interspecies encounters, specific phenomenal experiences, and abstract thinking patterns, essentially in the form of symbolic, cosmological, and ontological associations with large mammalian species and other material agents (Lev and Barkai, 2016; Zutovski and Barkai, 2016; Barkai, 2021; Finkel and Barkai, 2024; Litov and Barkai, 2024a, 2024b; see also Barkai, 2020, for the putative symbolic and cosmological connotations of the hippopotamid bone handaxe from Konso). Not surprisingly, increased embodied entanglements with large animals during the ESA/LP and MSA/MP periods were also coupled with complex adaptive behaviours and cognitive capabilities exhibited by hominins in different geographical regions (Storm, 2012; Pante, 2013; Domínguez-Rodrigo et al., 2014; Organista et al., 2016; Barkai et al., 2017; Ingicco et al., 2018; Blasco et al., 2019; Altamura et al., 2020; Daujeard et al., 2020; Yravedra et al., 2021; Bhat et al., 2024; Mecozzi et al., 2025; Parfitt and Bello, 2026).

With regard to the spectrum of hominin-animal relationalities, the Neanderthals are likely to have been the epitome not only of behavioural and cognitive complexity but of organisms fully immersed in highly entangled and embodied associations with physicalities from the biological and inorganic realms. Being top-level carnivores (Jaouen et al., 2019; Dodat et al., 2025; but see Beasley et al., 2025, who challenge this long-lasting assumption, arguing that Neanderthals' high $\delta^{15}N$ values were likely caused by the consumption of rotting maggoty meat), these hominins appear to have devised high levels of adaptive behaviour and sophisticated technological and socio-structural mechanisms to manage the highly cognitively demanding trophic niche; this, in turn, has further unfolded elevated forms of interspecies intimacy and potential phenomenal qualities highly contingent on patterns of hominin-matter proximity. In this respect, by ~300 and 50 ka, Neanderthals from different Middle Paleolithic archaeological sites in Eurasia (e.g., Les Pradelles [France], Lehringen, Neumark-Nord, Schöningen [Germany], Velika Balanica cave [Serbia], and Amud and Kebara caves [Israel]) evince high levels of embodied engagement with animals and other material agents exemplified by the cooperative and/or communal hunting of large mammals (horses [*Equus mosbachensis*], reindeer [*Rangifer tarandus*], straight-tusked elephants [*Palaeoloxodon antiquus*]) and a wide range of complex technological and socio-ecological behaviour in the form of adaptations to novel ecological settings (e.g., rugged mountainous terrain) and prey type (e.g., ibex, *Capra ibex*), crafting and utilisation of wooden throwing/thrusting spears and bone tools, culturally transmitted patterns of carcass processing, and large-scale exploitation of within-bone nutrients (Thieme, 1997; Costamagno et al., 2006; Gaudzinski-Windheuser et al., 2018, 2023a, 2023b; Conard et al., 2020; Leder et al., 2024; Hutson et al., 2024, 2025; Mateo-Lomba et al., 2024; Doyon et al., 2025; Jallon et al., 2025; Kindler et al., 2025; Milošević et al., 2025; Armaroli et al., 2026; Téllez et al., 2026; Verheijen et al., 2026).

With respect to Neanderthal tool-assisted hunting, for instance, an experimental study led by Bebber et al. (2024) suggests that the velocity and kinetic impact energy of throwing spears would have further increased whenever high topographic and/or biological relieves were exploited during hunting activities, thus underscoring the optimal weapon choice and adaptive behaviour demonstrated by our closest fossil relatives. After all, the cognitive, social, and technological underpinnings of communal hunting of large animals likely emerged approximately 400,000 years ago (or even earlier) in pre-Neanderthal populations (Rodríguez-Hidalgo et al., 2017), a pattern of behaviour that has been exhibited until recent times by modern Indigenous peoples of the Americas, Africa, and Oceania (Morin et al., 2024).

Notably, Kindler et al. (2025) have recently reported that Neanderthals from the site of Neumark-Nord (~125 ka) also devoted extensively to the extraction of within-bone lipids; hence, together with the consumption of maggoty and putrid meat (Beasley et al., 2025; Piñero and Librado, 2026) and herbivore stomach contents (Buck and Stringer, 2014; Buck et al., 2016), these sophisticated forms of grease rendering exhibited by Neanderthals (and possibly by earlier hominin populations like those yielded by Qesem Cave, Israel [~430 ka]; Blasco et al., 2024) may well have functioned as critical adaptive strategies to cope with the nutritional challenges posed by diets based heavily on animal foods (i.e., "rabbit starvation" [exceeding the ~300 g of dietary protein per day] and scurvy [vitamin C deficiency]), as documented by the ethnohistoric accounts of the arctic and subarctic foragers (Speth, 2017, 2019, 2025).

In summary, the abovementioned evidence of Neanderthal behaviour might thus point to (1) the maximization of hominin cooperative hunting strategies (e.g., Morin et al., 2024); (2) the development of sophisticated adaptive mechanisms to operate effectively within varying ecological niches; (3) the mindful exploitation of the mechanical and structural properties of plant materials for the crafting of spears, a pattern which likely represents a complexification of the termite fishing probes made by chimpanzees (Pascual-Garrido et al., 2025); (4) the deployment of highly adaptive patterns of processing and consumption of nutrient-rich animal products (e.g., putrefied meat and fat), akin to those exhibited until quite recently by northern latitude and even tropical small-scale societies (Speth, 2017, 2019, 2024, 2025; Speth and Morin, 2022); and (5) increased levels of association with megaherbivores and other large mammalian prey—as evidenced, e.g., by complex interactions with osseous materials—that likely go beyond trophic dynamics and other utilitarian aspects. From an embodied and relational viewpoint, therefore, the patterns of behaviour, ecological knowledge, and sophisticated cognitive capabilities exhibited by Neanderthals may also unveil intimate forms of organism-environment interactions deeply embedded in ecological niches characterised by the continuous compenetration of matter and agentic properties. These enmeshments of materialities and elevated interspecies intimacy—including highly embodied and multi-sensory engagements with mammals, insects, plants, and inorganic matter—may have set the stage for the evolution of ritual, cosmological, and ontological systems and activation of higher-order relational processes.

5.4. Beyond trophic dynamics and material interactions: metaphysical assumptions and forms of theorising on animal matter

Spanning the MP/MSA and the present, the final stage exhibits heightened embodied and cognitive-sensory engagements with large-sized mammals, thus primarily implicating complex interspecies relational dynamics, technological sophistication, and elaborate conceptual systems. Throughout the MP/MSA and Upper Paleolithic periods, for example, a wide range of osseous materials were shaped into complex tools, engraved with abstract patterns occasionally filled with ochre, and possibly endowed with symbolic and ritual properties, mainly by Neanderthals, Denisovans, and anatomically modern humans (d'Errico et al., 2001; d'Errico and Henshilwood, 2007; Germonpré and Hämäläinen, 2007; Abrams et al., 2014; Zhang et al., 2016; Majkić

et al., 2018; Li et al., 2019; Shaham et al., 2019; Shunkov et al., 2020; Leder et al., 2021; Prévost et al., 2022; Baquedano et al., 2023; Płonka et al., 2024; Golovanova et al., 2025; Talamo et al., 2025). It is noteworthy that, apart from the symbolic and ritual significance ascribed to those osseous artefacts, higher-order relational processes are likely to have been at stake within animal-hominin connections. Theoretically, the trophic system—characterised by a high degree of exposure to organismic interactions and intimate compenetration of physicalities—appears to have moulded higher-order categories of phenomenal experience (Abad Espinoza, 2022); prehistoric lifeworlds and metaphysical presuppositions may indeed have been the theoretical backdrop supporting the continuity of complex and highly embodied forms of associations between elements of the material world and their agentic properties.

Within the framework of prehistoric modes of embodiment in the animal-hominin interface, the ~120 ka engraved aurochs (*Bos primigenius*) bone shaft by hominins in the Levant (Prévost et al., 2022), the ~43 ka accumulation of large herbivore crania (e.g., *Bison priscus*, *Bos primigenius*, *Stephanorhinus hemitoechus*) by Neanderthals in central Spain (Baquedano et al., 2023), the ~40 ka decorated mammoth (*Mammuthus primigenius*) tusk boomerang by *Homo sapiens* at Obłazowa Cave, Poland (Talamo et al., 2025), the Eurasian elk (*Alces alces*) engraved tooth pendant from the Mesolithic burial at Donkalnis, Lithuania (Butrimas et al., 2025), and the red deer antler 'masks' from the Mesolithic site of Star Carr in northern England (Conneller, 2004) stand out as prominent examples of particular forms of hominin-animal intimacies, epitomised by bodily and sensuous interactions and likely imbued with ritual, mytho-cosmological, and ontological dimensions. Nevertheless, those forms of conceptualising animals and ontological associations likely arose in the Lower Palaeolithic (Lev and Barkai, 2016; Zutovski and Barkai, 2016; Barkai, 2020, 2021; Finkel and Barkai, 2024; Litov & Barkai, 2024), paving the way for the further construction of a zoontological framework that puts animal prey at the centre of complex cosmic and ritual negotiations (Viveiros de Castro, 1998; Bird-David, 1999; Hill, 2011, 2013; Descola, 2013; Overton and Hamilakis, 2013; Guenther, 2015; Cauteren, 2020; Ingold, 2021; Agarwal, 2026).

The archaeological and ethnographic records of modern foragers further corroborate the operation of these superstructural mechanisms. Specifically, notions of food taboos and a wide variety of rituals—from the special treatment of animal skeletal remains and body parts to negotiations with shamans and immaterial entities like game masters—are to be found in the Amazon (e.g., Tukanoans: Reichel-Dolmatoff, 1985; Yukuna: Van der Hammen, 1992; Huaorani: Rival, 1996; Juruna: Lima, 1999; Nukak: Politis and Saunders, 2002; Shuar: Abad Espinoza, 2025); in Mesoamerica (e.g., Maya: Brown, 2005; Brown and Emery, 2008); in the Arctic and Boreal regions (e.g., Ojibwa: Hallowell, 1960; Mistassini Cree: Tanner, 1979; Rock Cree: Brightman, 1993; Inuit: Turner, 1990; Yukaghirs: Willerslev, 2004); in Africa (e.g., Nuer: Howell, 1945; Ikoma: Kideghesho, 2008; Baka: Joiris, 1993; Hirata et al., 2010; Yasuoka, 2021; San: Lewis-Williams and Biesele, 1978; McGranaghan and Challis, 2016; Guenther, 2015); and in Asia and Oceania (e.g., Huaulu: Valeri, 2001; Torres Strait Islanders: McNiven and Feldman, 2003; Ainu: Masuda et al., 2006). In short, elevated embodied and sensory engagements with the largest mammalian prey species relative to the specificities of the above-mentioned ecological regions—ranging from elephants to eland (*Tragelaphus oryx*) to cetaceans and dugongs (*Dugong dugon*) to peccaries (Tayassuidae) and tapirs (*Tapirus* spp.) to bears (*Ursus* spp.) and elk—, coupled with a profound knowledge of animal morphology, behavioural ecology, and cognition, appear to have shaped the socio-structural and theoretical apparatus of indigenous societies worldwide.

Rock art has added a further layer of behavioural and cognitive complexity within the sphere of human-animal entanglements. Probably reflecting a complexification of forms of human-matter associations via non-figurative paintings—for example, the ~67.8 ka and ~65 ka hand stencils likely attributed to modern humans in Sulawesi, Indonesia and Neanderthals in Spain, respectively (Hoffmann et al., 2018; Oktaviana et al., 2026)—depictions of animals during the Late Pleistocene by modern humans in Europe (Bacon et al., 2023; Barkai et al., 2024), Indonesia (Aubert et al., 2019; Brumm et al., 2021; Oktaviana et al., 2024), and the Amazon (Morcote-Ríos et al., 2021;Iriarte et al., 2022; Hampson et al., 2024; Robinson et al., 2024) may have functioned as concrete manifestations of conceptual schemas that regarded animals (including extinct megafauna) as more than materialities for trophic exchanges and/or triggers of aesthetic capacities. For example, amongst ancient Near Eastern cultures, the ibex appears conspicuously in rock art (and other forms of engravings), thus further attesting the primary role of this animal within their symbolic, ritual, mytho-cosmological, and ontological systems (Avner et al., 2017; Torkamandi et al., 2025). Interestingly, these distinct forms of conveying the properties of game animals through rock paintings are also exhibited by modern Indigenous peoples, such as the hunter-gatherer populations of Northern Fennoscandia (Lahelma, 2019) and the San of southern Africa (McGranaghan and Challis, 2016). These creative expressions therefore reveal maximum compenetration of physicalities and agential qualities that, from the metaphysics of ancient and modern hunter-gatherers, may have represented interrelated levels of ontological associations between humans, animals, and other existents from the physical and spiritual realms.

The Amazonian case is noteworthy in this regard because rock depictions hint at ancient relations with megafauna that likely laid the foundation for the further configuration of superstructural mechanisms underpinning current patterns of human-animal interactions. High levels of bodily and cognitive-sensory engagement with giant ground sloths (e.g., *Glossotherium*, *Megatherium*) instantiated by Late Pleistocene trophic dynamics (e.g., Prates et al., 2025), bone ornaments (Pansani et al., 2023) and rock paintings (Iriarte et al., 2022) could, for example, shed light on current forms of interspecies intimacy and associated mytho-cosmological and ontological frameworks; the sloth as a pervasive figure in Amazonian mythology (Lévi-Strauss, 1988), as well as concepts of dietary taboos and ritual performances—in the form of complex negotiations with prey, shamans, and spiritual forces relating to certain mammals, i.e., particularly those of medium and large size: tapir, peccary, deer (Ross, 1978; Reichel-Dolmatoff, 1985; Van der Hammen, 1992; Rival, 1996; Lima, 1999; Politis and Saunders, 2002; Fausto, 2007; Abad Espinoza, 2025a)—may well have stemmed from ancient patterns of human-megafauna entanglements, exemplified by highly embodied forms of interspecies interactions, social and emotional bonding (e.g., Halfon and Barkai, 2020), and intense perceptual experiences. Hence, together with complex relations established with carbohydrate-rich tubers—characterised by intense organismic interactions involving different ontological planes and immaterial beings (Abad Espinoza, 2025b)—, these likely regulatory devices for the respect and preservation of prey (protein- and fat-rich sources), as well as the accentuation of animals' agentic and metaphysical properties, may thus represent the maximum manifestation of adaptive behaviour and abstract thinking developed in this novel tropical rainforest biome colonised by humans. In summary, the quest for the procurement of nutrient-dense foods and, consequently, the gradual complexification (behavioural and socio-cognitive) and intensification of hominin-animal associations may denote an evolutionary scenario where the predatory pattern of our primate relatives seems to have amplified in such a way as to incorporate modes of relations made manifest beyond physical realities.

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